Annual Variation in Bee Community Structure in the Context of Disturbance (Niagara Region, South-Western Ontario)

by

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ABSTRACT

This study examined annual variation in phenology, abundance and diversity of a bee community during 2003, 2004, 2006, and 2008 in recovered landscapes at the southern end of St. Catharines, Ontario, Canada. Overall, 8139 individuals were collected from 26 genera and sub-genera and at least 57 species. These individuals belonged to the 5 families found in eastern North America (Andrenidae, Apidae, Colletidae, Halictidae and Megachilidae). The bee community was characterized by three distinct periods of flight activity over the four years studied (early spring, late spring/early summer, and late summer). The number of bees collected in spring was significantly higher than those collected in summer. In 2003 and 2006 abundance was higher, seasons started earlier and lasted longer than in 2004 and 2008, as a result of annual rainfall fluctuations. Differences in abundance for low and high disturbance sites decreased with years. Annual trends of generic richness resembled those detected for species. Likewise, similarity in genus and species composition decreased with time. Abundant and common taxa (13 genera and 18 species) were more persistent than rarer taxa being largely responsible for the annual fluctuations of the overall community. Numerous species were sporadic or newly introduced. The invasive species *Anthidium oblongatum* was first recorded in Niagara in 2006 and 2008. Previously detected seasonal variation patterns were confirmed. Furthermore, this study contributed to improve our knowledge of temporal dynamics of bee communities. Understanding temporal variation in bee communities is relevant to assessing impacts caused on their habitats by diverse disturbances.

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A mis abuelas, y a todas aquellas personas que no pudieron estudiar en su infancia

And to the effort of the peoples of the two continents where I have studied

"Culture, which makes talent shine, is not completely ours either, nor can we place it solely at our disposal. Rather, it belongs mainly to our country, which gave it to us, and to humanity, from which we receive it as a birthright"

José Martí

"La cultura, por lo que el talento brilla, tampoco es nuestra por entero, ni podemos disponer de ella para nuestro bien, sino es principalmente de nuestra patria, que nos la dió, y de la humanidad, a quien heredamos"

José Martí

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CHAPTER I: ANNUAL VARIATION IN BEE COMMUNITY STRUCTURE

1. INTRODUCTION AND LITERATURE REVIEW

1.1. The Carolinian Zone and the Niagara Region

This study was carried out in the Carolinian Zone, south-western Ontario, which concentrates the majority of the rare plant species of Ontario and forms a continuum biome with the Eastern Deciduous Forest of North America (Argus, 1992). The Niagara Region forms part of the eastern edge of the Carolinian Zone, an 1800 km^2 area of a high ecological value originally composed of prairies, meadows and woodland communities of which 97% have been already degraded (Argus, 1992; Van Hemessen, 1993, *in* Rutgers-Kelly, 2005). Relatively undisturbed patches of natural or naturalising woodland edges, grasslands and meadows may serve as both ecological refuges and habitat sources where the flora and the associated insect fauna find shelter and may expand (Richards *et al.*, 2011). Franzén and Nilsson (2010) have found that the patch size is indirectly linked to bee community abundance through its influence on host plant population sizes. Therefore, the quality of these ecological refuges may help to protect bee communities of the Niagara Region from detrimental effects that anthropogenic disturbances cause to the availability of food and nesting resources (Argus, 1992; Roulston and Goodell, 2011). In small and relatively undisturbed patches, bee species composition correlates better to habitat change produced by anthropogenic disturbance than does non-bee pollinator species composition (Quintero *et al.*, 2010). Furthermore as Kevan (1999) suggested, bee communities could also have the potential of becoming a bioindicator of habitat change, with interest for conservation purposes.

1.2. The importance of bee communities

Bees (Hymenoptera, Apoidea) are particularly diverse, accounting for 20,000 to 30,000 species worldwide, with an elevated number of rare species (Michener, 2000; Williams *et al.,* 2001). In addition, bees constitute the main pollinator group in many ecosystems including agricultural habitats, and play a significant ecological and economic role (Cane, 2001; Kevan, 1999; Michener, 1979; Potts *et al.*, 2003a; Williams *et al.,* 2001). Bee communities enhance the maintenance of biodiversity through their role in the sexual reproduction of 90% of angiosperm plants (Fontaine *et al.*, 2008; Kearns *et al.*, 1998; Kevan, 1999; Potts *et al.*, 2003a). Despite their importance as pollinators, only recently has the effect of anthropogenic disturbance been studied on a bee community of Niagara (Rutgers-Kelly, 2005; Richards *et al.,* 2011). Furthermore, this is the first study in this region, investigating patterns of annual variation in a bee community.

1.3. Temporal variation in animal communities

The number of species co-existing in a community is determined by oscillations in abiotic and biotic factors over time (Chesson and Huntly, 1989; Dupont *et al.,* 2009; Fraterrigo and Rousak, 2008; Kallimanis *et al.,* 2009; Kevan, 1999; Preston, 1960; Sousa, 1984). The abiotic factors may include temperature, humidity, nutrient supply, soil chemistry, living space, and (natural or anthropogenic) disturbance. The biotic factors include competition, predation, parasitism, and mutualism. As a result of the dynamic nature of the above factors, community variability in abundance and diversity tends to increase with time (Hanski, 1990). Several studies have found that temporal community variation is related to fluctuations in abundance (den Boer, 1981; Hanski, 1982a, 1990;

Taylor and Woiwod, 1980). These changes would be more noticeable in abundant species which are more variable than rare species (Glazier, 1986; Gaston, 1998; Owen and Gilbert, 1989; Wolda, 1983). However, abundant species over time tend to be more persistent and their proportional representation within the community is also more stable than in rare species (Collins and Glenn, 1991; Durrer and Schmid-Hempel, 1995; Gibson *et al.*, 1999; Guo *et al.*, 2000; Hanski, 1982b,c).

Temporal variation has been described for a diverse array of animal communities including aphids, aquatic invertebrates, bees, birds, carabid beetles, lizards, moths, rodents, syrphid flies and tropical insects (Cam *et al.*, 2000; Connell and Sousa, 1983; den Boer, 1981; Glazier, 1986; Ostfeld, 1988; Owen and Gilbert, 1989; Roubik, 2001; Schoener, 1985; Taylor and Woiwod, 1980; Taylor *et al.*, 1980; Wolda, 1983). The above studies reported a great deal of temporal variability in structure for animal communities. This included variation in the number of species and their relative abundances, and changes in their morphological, physiological and behavioural traits. Knowledge of temporal variation patterns is still being built; hence comparisons among animal communities may offer valuable insights for understanding these processes (Hanski, 1990). Furthermore, related animal communities may display similar temporal variation patterns (Hanski, 1982a, 1990; Taylor *et al.*, 1980). Several studies recognised that arthropod communities experience a greater temporal variation than other animal communities (i.e. vertebrates) (den Boer, 1981; Hanski, 1990; Ostfeld, 1988; Owen and Gilbert, 1989; Schoener, 1985).

1.4. Temporal variation in bee communities

Bee community abundance and diversity are highly variable, with a high genus and species turnover over time (Dupont *et al.,* 2009; Grixti and Packer, 2006; Herrera, 1988; Minckley *et al.,* 1999; Petanidou *et al.,* 2008; Price *et al.,* 2005; Roubik, 2001; Williams *et al.,* 2001; Wilson *et al.,* 2009; Wolda and Roubik, 1986). It has been observed that bee community variability increases as the time scale increases (Cane *et al.*, 2005; Hanski, 1990; Petanidou *et al.,* 2008; Roubik, 2001; Williams *et al.,* 2001).

The phenology (or seasonal variation) of bee communities has been extensively studied (González *et al.,* 1999; Gordo and Sanz, 2006; Herrera, 1988; Kallimanis *et al.*, 2009; MacKay and Knerer 1979; Oertli *et al.*, 2005; Ortiz and Belda, 1994; Richards *et al.*, 2011; Rutgers-Kelly, 2005; Tuell *et al.*, 2009; Tylianakis *et al.*, 2005). Seasonal weather variability produces fluctuations of flowering and nesting resources, which in turn influence bee behaviour and life cycles (Gordo and Sanz, 2006; Herrera, 1988; Ortíz and Belda, 1994; Ortíz and Tinaut, 1994; Packer *et al.*, 1989; Richards and Packer, 1995; Roubik, 2001; Roulston and Goodell, 2011; Rutgers-Kelly, 2005). Bee communities are highly related to the time of the year in which floral resources become available (Gordo and Sanz, 2006; Herrera, 1988; Roulston and Goodell, 2011). Indeed, bivoltine and multivoltine species (having two or more brood generations per year, respectively) may show seasonal delays in population abundance in response to fluctuations of flowering resources (Roulston and Goodell, 2011).

An increasing body of literature analyses long-term variation of bee communities at annual and/or decadal scales (Alarcón *et al.*, 2008; Cane *et al.*, 2005; Fishbein and Venable, 1996; Grixti and Packer, 2006; Herrera, 1988; Minckley *et al.,* 1999; Petanidou

et al., 2008; Roubik, 2001; Tepedino and Stanton, 1981; Williams *et al.,* 2001). In order to analyse annual variation in abundance and diversity in bee communities, studies should meet certain methodological requirements (Cane and Tepedino, 2001; Roubik, 2001; Williams *et al.,* 2001). To measure the variability in abundance and diversity, it is necessary to have an adequate inventory of the total number of individuals and species in the community (McArdle and Gaston, 1993; Williams *et al.*, 2001). Annual variation processes need to be studied in the long-term, and a sufficient number of replications (covering at least three years) should be provided in order to describe any trend (Roubik, 2001). In addition, the use of standardised methods ensures the uniformity of the collected data and the repeatability of the study (Cane and Tepedino, 2001; Roubik, 2001; Williams *et al.,* 2001). This is especially important for re-sampling studies that re-visit a previously surveyed location after several decades, such as that of Grixti and Packer (2006). Below, studies that approach these criteria in their analyses of the annual abundance and diversity variation of bee communities are reviewed.

1.4.1. Annual variation in the bee community of Caledon Hills

A re-sampling study was made at Caledon Hills (SW Ontario), a Carolinian Zone location initially sampled in 1968 and 1969 by MacKay and Knerer (1979). Between those earlier collections and these of Grixti and Packer (2006) in 2002 and 2003, 34 years had elapsed. Grixti and Packer (2006) made an inventory of species providing full details of the Caledon Hills bee community sampled in both periods. In the earlier study 9,784 bees belonging to 5 families, 26 genera and 105 species were collected. As for the second study, 10,437 bees belonging to 5 families, 27 genera and 150 species were collected.

From the total of bees collected during the first study nearly two thirds were collected in 1968 (6290 bees) and over one third (3494 bees) in 1969, which represented a 56% decline from one year to the next. Conversely, during the second study at Caledon Hills the number of bees collected was 4293 and 6144 in 2002 and 2003, respectively, which represented a 70% increase in just one year. In addition, the Caledon Hills bee community experienced an average change of 8.2 times in relative abundance between studies. This outcome was mostly produced by the decline of *Lasioglossum imitatum* from 5673 to 96 bees between both studies. Relative abundance also varied drastically for species such as *Ceratina calcarata*, which increased from three to 795 bees, *Andrena wilkella*, which increased from 24 to 1162 bees and *Colletes kincaidii* which declined from 35 to one bee.

A total of 165 species was collected during both studies. The number of species increased from 105 to 150 species between studies. Sorting by years, 98 species were collected in 1968, 76 species in 1969, 98 species in 2002, and 143 species in 2003. Ninety species (86%) were shared between the first and the second studies, although the community similarity, using the Morisita-Horn index, was only 7.5%. However, inter-annual similarity was much higher, with 99% similarity between 1968 and 1969 and 76% similarity between 2002 and 2003. In general, there was an increase in species richness and diversity indices (i.e. Shannon-Wiener and Evenness) for almost all guilds considered between the first and the second studies, namely ground-nesting, parasitic, non-parasitic, pollen generalist, native, and exotic species.

The vegetation of both studies consisted of pioneer or early successional stages, formed by mats of regularly mowed grass, along with patches of flowering plants (Grixti

and Packer, 2006; MacKay and Knerer, 1979). In addition, mature trees and shrubs were also found in both periods (such as *Prunus* sp. and *Cornus* spp. of great importance to bees), which Grixti and Packer (2006) assigned to mid-successional plant communities. In both studies, the vegetation covering the ground varied from very light to very dense (Grixti and Packer, 2006; MacKay and Knerer, 1979). Soil conditions also remained similar in both periods, ranging from sandy and loose to quite compact and cohesive. The soil was mostly formed of mixed rocks and pebbles, which facilitated the drainage as no standing water was noted even after heavy rains (MacKay and Knerer, 1979). Moreover, the site had a large area of ground with a southern exposure and a wide slope gradient. These soil conditions offered ground-nesting species a wide variety of nesting sites, and protection against nest flooding if rainfall occurred during the breeding seasons (MacKay and Knerer, 1979; Richards and Packer, 1995, 1996; Richards, 2004). Thus, edaphic factors mostly benefited ground-nesting species (which predominated in both studies), while floral resource availability may have enhanced the diversity of the overall Caledon Hills bee community (Roulston and Goodell, 2011; MacKay and Knerer, 1979).

Grixti and Packer (2006) suggested that the Caledon Hills bee community had been subject to ecological succession. However, the following arguments support the interpretation of annual variation. Plant inventories in both studies were incomplete, omitting several species of flowering plants and trees. This jeopardised the comparison of vegetation between periods and did not provide sufficient evidence of plant community succession. In both studies, the presence of mature trees and shrubs was recorded; in addition, habitat management practices such as mowing took also place. In the case of an on-going ecological succession process between the two studies, the species richness of

pollen specialists and wood nesting species should have also varied. Moreover, diversity changes in other guilds seem to be better explained by changes in relative abundance of guilds between studies. It should also be noted that the greater species richness registered in the second studied was likely influenced by the high number of bees collected.

Richardson and Richards (2008) analysed the effect that abundance had on diversity of the Caledon Hills bee community. Their results support the interpretation of annual variation. They used the dataset provided by Grixti and Packer (2006) and tested variation in species richness both among years and studies. Grixti and Packer (2006) had performed a rarefaction analysis for testing the variation of species richness, which limited the number of individuals analysed to the sample size of the smallest sample. Instead, Richardson and Richards (2008) performed a randomisation analysis which allowed using the complete dataset. This analysis tested the null hypothesis that differences in species richness were due to variation in abundance among temporal samples. When differences in species richness were analysed among years, Richardson and Richards (2008) found that the observed species richness was lower than expected for the years 1968, 1969 and 2002 and similar to the expected value for 2003. The year 2003, with 36 unique species found out of the total 165 species, was particularly more speciose than the other three sampling years. Therefore, given that differences were mostly due to the influence of one sampling year, annual variation in diversity seems to be a more plausible explanation of these results than ecological succession. Furthermore, this interpretation would be also in agreement with previous long-term studies of bee communities (Williams *et al.,* 2001; Cane *et al.*, 2005; Roubik, 2001).

1.4.2. Annual variation in desert bee communities

In the southwestern U.S.A., the desert bee fauna related to the bush *Larrea tridentata* was studied by Cane *et al.* (2005), who re-sampled the same sites in three different regions (Lower and Upper Sonoran Deserts and the Chihuahuan Desert) during 3 consecutive years. *Larrea tridentata* blooms in spring for about 55 days and in summer sporadically in response to rains (Bowers and Dimmit, 1994). Flowers of *L. tridentata* remain open for a maximum of 2 days (Minckley *et al.*, 1999). Drought prevents flowering and severely diminishes bee populations (Bowers and Dimmit, 1994; Hurd and Linsley, 1975), although no drought episode was reported by Cane *et al.* (2005). Sites consisted of 1 ha plots with flat *L. tridentata* stands that were more than one-third through their blooming season (Cane *et al.*, 2005; Minckley *et al.*, 1999). Bush canopy volume and density per hectare varied greatly across sites; floral resource variation could lead to changes in species richness, although no differences were found (Minckley *et al.*, 1999; Roulston *et al.*, 2011).

Over the three-year study, between 54 and 68 species were collected per site. Inter-annual diversity comparisons were made using pairs of consecutive years. In the above sites, species richness was quite low, ranging from 5 to 23 species per year, with 73% annual similarity in species composition (using the Morisita-Horn index). In addition, one extra Upper Sonoran site was re-sampled during five consecutive years, and inter-annual comparisons of diversity were made. In this site, a total of 19 species was collected, with 7 to 12 species in any given year. Among these species, only 3 of them were caught in all years, while between 5 and 8 species were shared among consecutive year pairs. The similarity of species composition among the five consecutive years was

87%, lower than the seasonal similarity of species composition (97%). These results indicate that the *L. tridentata* bee community was temporally stable. The high temporal stability of species may be enhanced by the limited bee foraging range and the isolation of populations caused by habitat fragmentation (Bommarco *et al.,* 2010; Cane *et al.,* 2006; Zurbuchen *et al.,* 2010).

At a regional scale, Cane *et al.* (2005) found that thirteen abundant species were more persistent and more frequently collected (with 76% of the total number of bees) than rare species during paired or multiple years. Cane *et al.* (2005) also reported that the thirteen abundant species formed a diverse group with representation of all the North-American families and several nesting guilds. Alternatively, half of the oligolectic (pollen specialist) species on *L. tridentata* were less common and unique to one collection year, while the remaining half were represented in pairs of years. Oligolectic species on *L. tridentata* may be more susceptible to inter-annual changes in resource quantity than the thirteen abundant species (Minckley *et al.*, 1999). In *L. tridentata*, the spring bloom is longer, and its timing is more predictable than the sporadic summer bloom as a result of more consistent rainfall patterns during winter and spring than during summer (Bowers and Dimmit, 1994; Hurd and Linsley, 1975). This is reflected by the fact that all oligolectic species are active in spring, while only three of them emerge during summer blooms (Bowers and Dimmit, 1994; Hurd and Linsley, 1975). Therefore, a small cohort of abundant and persistent species was responsible for most of the flower visits, while very few flower visits were carried out by a majority of rare and transient species.

1.4.3. Annual family-level variation in an Appalachian bee community

Studies of annual variation in bee communities at the family level are relatively scarce. In a two-year study performed in the Appalachian shale barrens, Kalhorn *et al.* (2003) collected 841 bees in 1992 and 361 bees in 1993 using malaise traps. In both years, plant density and species composition varied seasonally; dense flower patches occurred in spring when moisture was higher and the vast majority of the bees were trapped. Nonetheless, Kalhorn *et al.* (2003) reported no annual changes in their bee surveys and plant inventories due to dry periods during 1992 and 1993. No inter-annual variation was detected in the number of bees collected per family (paired t-test: $t_5 = 1.56$, $p = 0.180$). The family rank only varied for the rarest families, namely Colletidae (7 bees in both years), Megachilidae (4 bees), and Melittidae (4 bees). The most abundant families were Halictidae with a total of 690 bees in both years (representing 54% of the total number of bees in 1992 and 66% in 1993), Andrenidae with 471 bees (comprising 44% of the total number of bees in 1992, and 28% in 1993), and Apidae with 26 bees (2% and 4% in 1992 and 1993, respectively).

1.4.4. Annual variation in a rainforest bee community

Roubik (2001) sampled an orchid bee population in a lowland rainforest for a 20-year period, in which over 47,000 bees were registered in 1952 monthly counts. Annual variation in abundance by two to four-fold was frequently detected for the overall bee community abundance, reaching up to fourteen-fold for some species. The El Niño-Southern Oscillation climatic events (in 1982-1983, 1992 and 1997) did not substantially affect the orchid bee population, with only brief seasonal increases in bee abundance.

Despite the marked annual variation of abundance, no changes in diversity were detected from the year 1980 to 2000, for a total of 32 species. The annual variation trends of bee communities in tropical regions may differ from those observed in temperate climates. Comparing this to the above studies, the annual patterns of diversity for tropical bee communities would seem to be more stable than for bee communities of temperate regions. This is in agreement with previous observations by Wolda (1983) and Wolda and Roubik (1986) who found tropical bee communities to be more stable than their temperate counterparts.

1.4.5. Bee community variation among decades

Currently, very few studies have been made on a decades-long basis, collecting continuously throughout a sufficiently long annual series (Roubik, 2001; Cane *et al.*, 2005). However, in order to gain an improved understanding of long-term variation processes related to bee communities, studies should ideally be extended over periods greater than a few years (Roubik, 2001). Furthermore, variation patterns detected at the year-level should be more noticeable at the decade-level (Roubik, 2001).

1.4.5.1. Decadal variation of desert bee communities

Cane *et al.* (2005) re-sampled the *L. tridentata* bee community at six sites in the southwestern U.S.A. that were initially studied by Hurd and Linsley (1975). Many species of the *L. tridentata* bee community persisted between decades with half of the species shared by the two previous studies. The similarity in species composition between the two decades was 36% (Morisita-Horn index). Not surprisingly, the similarity

in species composition was lower between decades than among years (87%). However, Cane *et al.* (2005) regarded the actual similarity between decades as under-estimated given that the two studies differed in their sampling effort. This likely caused the abundance to be lower for several common species, and some rare species were missing from the more recent and less intensively sampled study.

1.4.5.2. Decadal variation in a Michigan bee community

Williams *et al.* (2001) analysed un-published data of a bee community studied by F.C. Evans for 40 years at the E.S. George Reserve in Michigan, USA. Although the Evans dataset presented some flaws such as some under-sampled years, it still allowed an analysis of the long-term variation of a bee community subject to low anthropogenic disturbance. In order to compare the similarity of species composition, three years were selected from each decade (1950s, 1970s and 1980s). These were also contrasted with the early 1970s (1972-1973) characterised by an especially high abundance. Williams *et al.* (2001) found a decreasing degree of similarity in species composition (using the Morisita-Horn index) of the bee community with decade. The species composition in the 1950s was 54% similar to the 1970s, (44% similar to the early 1970s) and 27% similar to the 1980s. In addition, the similarity of species composition in the 1970s was 90% and 69% similar to the early 1970s and to the 1980s, respectively. Thus, the analysis of Williams *et al.* (2001) provided evidence of an important species turnover among decades. This inter-decade species turnover was accompanied by an average 200% change in abundance of the bee community (Williams *et al.*, 2001). However, this study

did not provide a temporal reference that allowed tracing this change throughout the decades.

1.4.5.3. The Carlinville bee community from the 1880s to 1970s

Robertson (1929) recorded 296 bee species from 441 flowering plants occurring in Carlinville (Illinois, U.S.A.), which is a mesic temperate area (Minckley, 2008). Over 15,000 visits of several insect orders were registered between 1884 and 1916 (Robertson, 1929; Marlin and Laberge, 2001). From 1970 to 1972, Marlin and Laberge (2001) re-sampled the same area, focusing on the 24 most visited plant species, although 43 other plants were also sampled for a total of 163 collection hours. These authors aimed to collect all the visiting bee species, combining sweep netting with the use of a long-handled net, allowing them to capture bees flying over short trees (Marlin and Laberge, 2001). During the period between the two studies, the prairie habitat, initially representing 73% of the landscape, was transformed into agricultural lands (Marlin and Laberge, 2001). A total of 228 bee species was collected excluding *Apis mellifera*, *Bombus* spp. and parasitic species. Robertson collected 214 species including 74 not detected in the re-sampling survey that recorded 154 species (of which 14 were unique). Sixty-five per cent of the species of the historical survey were collected again by Marlin and Laberge (2001). These authors also compared the similarity in species composition between both surveys by calculating the Jaccard and Sorensen similarity indices, whose values were 0.614 and 0.761, respectively.

In addition, a combined total of 179 species (excluding the above mentioned taxa) was collected on the 24 most-visited plant species. In this case, the species richness of the

historical survey was 157 (29 unique species), very similar to the 150 species (22 unique species) of the re-sampling survey. Likewise, 82% of the species collected by Robertson on the 24 plant species were detected in the re-sampling survey. Accordingly, the values of the Jaccard and Sorensen similarity indices were higher 0.715 and 0.883 respectively. As a result, Marlin and Laberge (2001) concluded that the high degree of similarity between both Carlinville surveys reflected that the bee community had remained almost invariable from the 1880s to 1970s.

1.4.5.4. The bee community of Plummers Island from 1909 to 2006

Norden (2008) published a century-long survey performed on Plummers Island (Maryland, U.S.A.) by several collectors who made an inventory of the insect fauna (Brown and Bahr, 2008). Over the century-long period, the vegetation of the island progressively changed from open land to developed woodland; conversely, the adjacent mainland forests were cleared. The collecting methods and sampling effort were not fully described and also varied over the collection period. This prevents the possibility of performing meaningful analyses such as a test of temporal variation of abundance. From 1909 to 1925 bees were collected by hand nets; from 1950s to 1972 hand nets and hanging wooden-traps were used; over the 1980s three methods (hand nets, Malaise and pan traps) were employed; and from the 1990s to 2006 bees were collected by hand nets or pan traps (Brown and Bahr, 2008; Norden, 2008). During the century-long survey over 9,000 bees were collected, most of them between April and June. In 1985, 163 species belonging to 37 genera were recorded, while in 2006, 232 species from 41 genera were

collected. The species composition for the pooled 1920s – 1950s period was the same as in the 2000s, with the addition of only two invasive species.

1.4.5.5. Historical and re-sampling surveys of a Colorado bee community

The bee community of Boulder County (Colorado, U.S.A.) was first sampled between 1904 and 1907 by Cockerell, who collected 164 species (Kearns and Oliveras, 2008). The Boulder bee community was re-sampled between 2001 and 2005 when 5741 bees and 110 species were collected, with 22% of these species represented by only one individual (Kearns and Oliveras, 2008). During the course of a century, Boulder County changed from prairie habitat to urban landscape, with a significant portion of natural habitat surrounding the city (Kearns and Oliveras, 2008). For purposes of comparison, the species list of the historical survey was narrowed to 116 species by Kearns and Oliveras (2008). In addition to similar species richness, the number of species per genus did not differ significantly between the two studies. As a result, these authors stated that bee species diversity remained constant even though dramatic changes in landscape had occurred in the course of a century. Furthermore, Kearns and Oliveras (2008) suggested that bee resource availability had increased over that period, helping to conserve the bee community of Boulder County.

1.4.5.6. Analysis of historical studies on long-term bee community variation

The studies of Kearns and Oliveras (2008), Marlin and Laberge (2001) and Norden (2008) concluded that diversity remained constant for an extremely long period of time ranging from five decades to a century. This implied that the community changes

occurring in shorter terms would decrease as time increased. This interpretation clearly contradicts the inter-annual and inter-decadal studies described above.

Nonetheless, in order to accept this interpretation further evidence should have been provided, and an accurate long-term assessment solving some methodological problems should have been made. The three studies failed to provide strong evidence of how important habitat changes influenced the bee community. The methodologies of the three studies were not standardised or fully specified; historical surveys used one collecting technique that differed from the diverse techniques of the re-sampling studies (i.e. pan traps, sweep and hand nets). The objectives also varied: historical surveys aimed to make an inventory of the bee fauna, whereas re-sampling surveys sought to maximise diversity. In addition, unequal sampling effort between surveys of the three studies may have resulted in abundance and diversity differences. This was specifically the case for the species lists of the Carlinville and Boulder County historical surveys that were narrowed in order to allow comparisons with the re-sampling surveys. This potentially under-estimated the diversity differences between historical and re-sampling surveys of both studies, since more species were detected in the historical survey (with more individuals collected) than in the re-sampling survey. Moreover, the three studies made important conclusions but flawed conclusions on diversity, analysing only two temporal references, when at least three samplings are needed to identify trends in long-term variation processes (Roubik, 2001). Indeed, inter-annual analyses of the bee community (using the re-sampling surveys) could have provided additional annual comparisons to contrast to the historical surveys. The three historical surveys also lacked information on

relative abundance of species, which prevented the later authors from analysing the abundance variation among years.

Finally, none of the three studies provided complete evidence of both the abundance and diversity of long-term variation in bee communities. Hence, the conclusion of these articles that diversity remained constant for almost a century should be questioned, due to the lack of sufficient proof and consistent evidence to support it. This was the result of using surveys combining different, missing or not-specified methods and insufficient knowledge of temporal variation in the bee community. Bee communities assessed from historical sources may provide important information for making inventories; however, they should not be used for temporal variation analyses of bee communities when doubts about methodological homogeneity exist.

1.5. A bee community of the Niagara Region

In 2003, a survey was carried out in set-aside grasslands at the Glenridge Quarry Naturalization Site (GQNS) and the Brock University campus, it included the same sites used in the present study (refer to section 2.1) (Rutgers-Kelly, 2005; Richards *et al.*, 2011). Both areas are located in southern St. Catharines, on the southern crest of the Niagara Escarpment (this formation is a World Biosphere Reserve), and have naturalised habitat patches of several ages (Richards *et al.*, 2011). The nearby habitat covers forests, suburban gardens, highways with grassy edgings, pastures and cornfields (Richards *et al.*, 2011). The Brock University campus includes set-aside natural areas and grasslands that have been fallow and rarely mowed for the last 40 years. Conversely, intensive farming occurred at GQNS until about the 1960s, when it became a limestone quarry and

subsequently a landfill site from 1976 to 2001 (Richards *et al.,* 2011). In early 2003 the GQNS ecological restoration was completed; the area was capped with clay and filled with soil, creating a substrate on which Carolinian vegetation was planted (Rutgers-Kelly, 2005). Thus, a habitat suitable for pollinators was regenerated after several decades of intensive agricultural and industrial exploitation. Nonetheless, the GQNS suffered a severe loss of insect populations after the quarry exploitation started. Succession with colonisation of insects, other fauna and flora began after restoration of the GQNS (Rutgers-Kelly, 2005). In 2003, bee populations at the GQNS sites were practically non-existent, while those on the Brock University campus that had persisted for a long time were relatively diverse (Rutgers-Kelly, 2005). Over the years flower and nesting resources may have likely differed among sites of both areas, consequently affecting the bee community (Steffan-Dewenter and Schiele, 2008; Potts *et al.* 2003b).

Disturbance can be defined as a discrete, punctuated killing, displacement or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established (Sousa, 1984). The intensity, frequency and time since the last disturbance may affect the availability of resources, creating a trade-off between the ability of species to colonise and to compete (Connell, 1978; Mackey and Currie, 2000). Connell (1978) proposed the Intermediate Disturbance Hypothesis (IDH) in order to explain the effect of disturbance on species richness. When disturbance episodes are very intense, frequent or recent, only a few species are able to survive or to re-colonise after each episode, resulting in low diversity (Connell, 1978). In the case of no disturbance, competitive exclusion also decreases diversity as only the best competitor species would be able to persist in the long-term.

When disturbance levels are intermediate, habitat patch heterogeneity is elevated, and many species have opportunities to re-establish, including good competitor species and pioneer species with good dispersal abilities. Accordingly, the IDH predicts that the highest species richness occurs in areas of intermediate disturbance, followed by areas of low disturbance, with the lowest species richness found in areas of high disturbance (Connell, 1978).

Rutgers-Kelly (2005) examined how anthropogenic disturbance affected the abundance and diversity of the bee community. The above mentioned sites at the Brock University campus had been subject to comparatively lower disturbance intensities than the GQNS sites. In addition, the time for recovery of the set-aside old fields at the Brock University campus had been greater than for the recently restored grasslands at GQNS. Hence, Rutgers-Kelly (2005) assigned disturbance levels to the sites of both areas based on the disturbance intensity and time since the last event. Disturbance levels were regarded as low at sites of the Brock University campus, while intermediate and high levels were assigned to sites at GQNS (Rutgers-Kelly, 2005). These sites were the same as in the present study except for those at intermediate disturbance levels. The study of Rutgers-Kelly (2005) supported the IDH, as the number of species significantly varied among sites (even when abundance was controlled) and displayed the same pattern as above. Sites with intermediate levels of disturbance had the highest species richness and abundance, followed by sites at low and high levels of disturbance, respectively.

In 2003, this bee community was systematically sampled by using three collecting methods (i.e. pan traps, sweep nets and flower collections) at meadows subject to different disturbance levels (Rutgers-Kelly, 2005; Richards *et al.*, 2011). Over 15,733 bee

specimens were collected, representing 124 species and morphospecies, of which only 8 species were abundant while 23 species were rare. The bee community presented three peaks of high foraging activity throughout the early spring, late spring and mid-to-late summer. The foraging activity in spring was higher than in summer, decreasing markedly by week 11 coinciding with the summer solstice. This was due to the gap period between the brood provisioning carried out by the nest foundresses and the emergence of the second brood of eusocial and bivoltine species (Richards *et al.,* 2011). The most abundant families were Halictidae (56% of the total number of bees collected), Megachilidae (23%), and Apidae (13%), while the families Colletidae (5%) and Andrenidae (3%) were less common. The dominance of the family Halictidae over other families of this survey is suggested by the fact that halictids were more frequently captured in pan traps than are bees in other families (Cane *et al.,* 2000; Richards *et al.,* 2011). Indeed, if only sweep nets were considered the Apidae would appear to be the most abundant; therefore, different families are selectively captured by each collecting method (Richards *et al.,* 2011). Richards *et al.* (2011) suggested that this bee community experiences a high species turnover due to an elevated number of transient species occurring sporadically in some years. This would be a factor contributing to the annual variation of diversity in this bee community (Cane *et al.,* 2005; Gibbs and Sheffield, 2009; Grixti and Packer, 2006; McArdle and Gaston, 1992; Minckley *et al.,* 1999; Richards *et al.*, 2011).

1.6. Thesis objectives and hypotheses

This is the first study made in Canada that comprises a bee collection of four years (2003, 2004, 2006 and 2008) using only pan traps. Over this period, pan traps were

set in transect patterns differing in length and shape covering unequal areas, which might cause differences in sampling effort and specimen collection rates. Droege *et al.* (2010) and Tuell and Isaacs (2009) reported that differences in spatial configuration and distance among pan traps might influence the number of bees collected and subsequent abundance and diversity analyses. A preliminary objective of this study aimed to test whether differences in sampling effort among transect patterns might affect annual trends in bee abundance and diversity. Therefore, the null hypothesis was that the number of bees and species collected would not differ among the three transect patterns tested (P140, X050 and X140). Support for this hypothesis is presented in Appendix I.

The major objectives of this study were to identify annual variation in a bee community of the Niagara Region in terms of changes in phenology, abundance and diversity over the four years studied. For the phenological analysis of the four sampling years, previous reports made in this region had identified patterns of seasonal variation (Rutgers-Kelly, 2005; Richards *et al.*, 2011). My hypothesis was that seasonal flight activity for the overall community and the most abundant species would vary among years.

Regarding abundance, the study of Richards *et al.* (2011) was used to classify bees according to their proportional representation. Genera and species recorded in this study thus could be classified as abundant, common or rare. Based on Rutgers-Kelly (2005), I hypothesised that the number of bees collected over the four years studied, at low disturbance sites would be significantly higher than in high disturbance sites. A second hypothesis was that the most abundant genera (or species) would occur more consistently over the years and would not switch into other abundance categories as often

as their common and rare counterparts. I also aimed to assess which species of the bee community would display annual variation in abundance. Furthermore, I hypothesised that bee abundance would differ annually among sites and disturbance levels.

As for annual changes in bee diversity, I made the hypothesis that bee community diversity, considered as generic and species richness and by other measures such as family, nesting guild, social habit and voltinism, would vary among years. Based on previous hypotheses by Hanski (1990), Petanidou *et al.* (2008), and Williams *et al.* (2001) that genus and species composition would differ increasingly with time, I formulated the hypothesis that genus and species turnover would increase with years elapsed. Previous studies had shown a relationship between stability in relative abundance and the persistence of taxa over time (please refer to the section 1.3); hence, I hypothesised that abundance ranks for the most abundant genera and species would be more stable over the years than those of rarer genera and species.

2. METHODS

2.1. Study sites

This study was carried out in four sites at the GQNS and the Brock University campus in southern St. Catharines, Ontario, Canada, (Fig. 1). Their proximity, separated by only 1.3 km, ensured that weather conditions were equivalent among all sites. All sites covered approximately an area of one hectare.

Two sites were sampled in the GQNS: Pond (latitude: N 43°07.436', longitude: W 79°14.205') and St. Davids (latitude: N 43°07.352', longitude: W 79°14.044'). The Pond site was located on the northern aspect of a covered landfill approximately 200 m from an artificial pond, while the St. Davids site was located on the eastern aspect of the covered landfill. The GQNS was ecologically restored in 2003 as meadow after having been subjected to several kinds of anthropogenic disturbance for more than a century. First, intensive farming occurred until the 1960s, followed by a quarry of limestone and eventually serving as a landfill from 1976 to 2001.

The two sites at the south end of the Brock University campus were denominated as Brock North (BrockN; latitude: N 43°06.903', longitude: W 79°14.826') and Brock South (BrockS; latitude: N 43°06.733', longitude: W 79°14.781'). In the 1960's they became abandoned farm lands remaining as set-aside meadows. In summer 2003, following construction of a parking lot, the original BrockN site was destroyed by construction and replaced with the Brock West site (BrockW; latitude: N 43°06.787', longitude: W 79°14.831') (Rutgers-Kelly, 2005; Richards *et al.,* 2011). Since the two sites were very similar, they were treated as a single site (BrockNW).

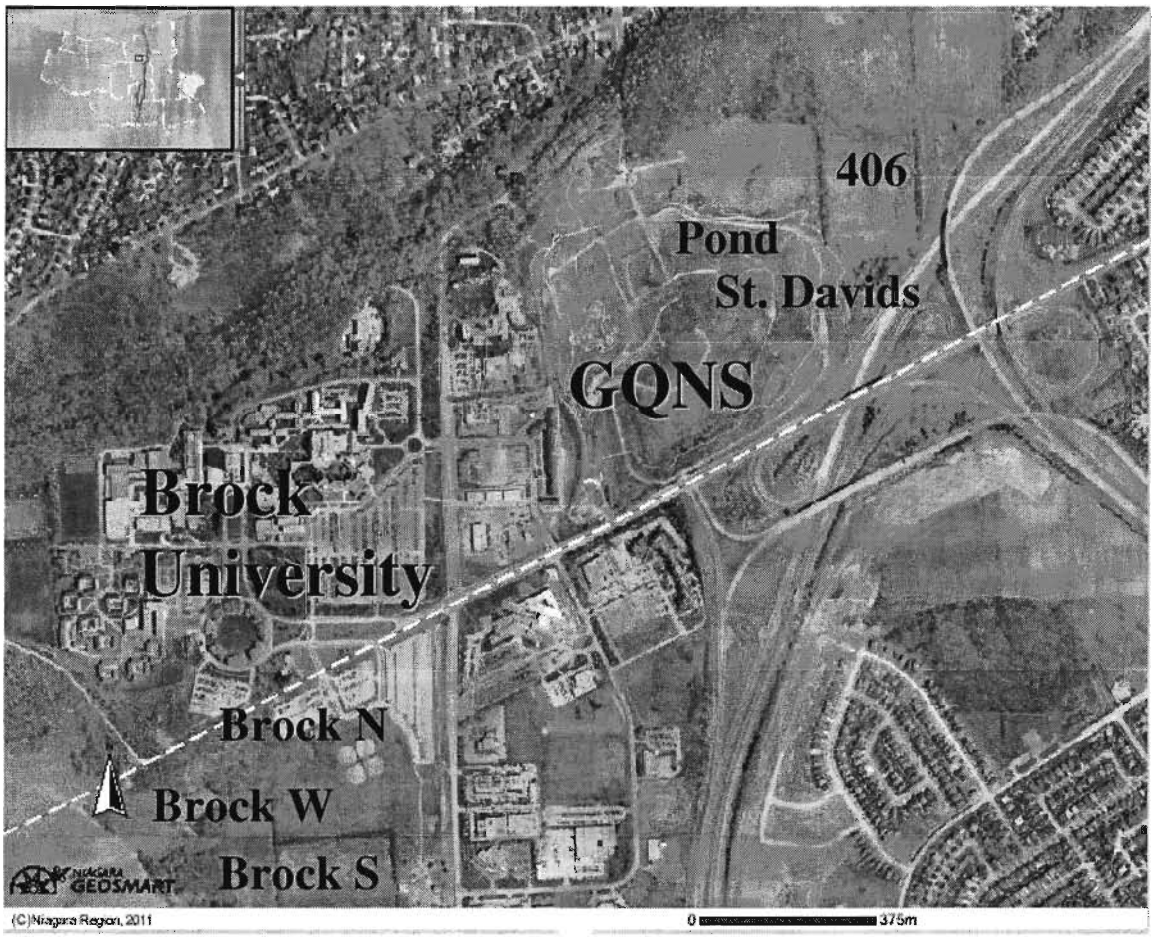


Fig. 1. Location of the study sites (small fonts) in relation to the Brock University campus and the Glenridge Quarry Naturalisation Site (large fonts). Note that when in 2003 construction at BrockN took place, it was substituted with BrockW and collections were pooled. The arrowhead in the lower left corner indicates north, while the box in the upper left corner indicates the relative position of the field sites within the Niagara Region. Photo credit: 2011 Niagara Navigator.

Comparatively, the four sites differed in the type and intensity of disturbance, in addition to the time since the last event occurred. Pond and St. Davids had been until recently subjected to intensive agricultural and industrial exploitation, while the old fields of the Brock University campus had been rarely disturbed for the last four decades (Rutgers-Kelly, 2005). In 2003 after the ecological restoration was completed, bee species began to re-colonise Pond and St. Davids, where they had been eradicated for the last 40 years (Rutgers-Kelly, 2005). In contrast, bee populations had persisted for several decades at BrockNW and BrockS, having sufficient time to recover from sporadic mowing (Rutgers-Kelly, 2005). Consequently, disturbance levels at Pond and St. Davids were categorised as high, while at BrockNW and BrockS were regarded as low.

2.2. Collection period of specimens

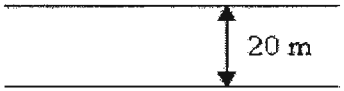
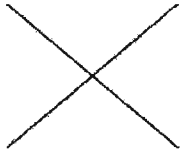
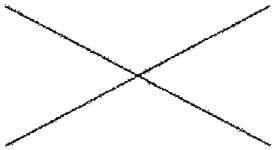
Bees collected using pan traps in 2003, 2004, 2006 and 2008 were used for the analysis of the bee community structure and its annual variation. Each year collections started by the last week of April (Week 1) and finished by the last week of September (Week 23). During 2003 and 2004 all sites were sampled bi-weekly, while during 2006 and 2008 the frequency of collection was weekly. When sampling was interrupted by rain, the collection was usually repeated within the same 7 to 10 day period. For analyses that require equal sampling effort among years, the dataset of four years was based on bi-weekly collections, usually from odd-numbered weeks. However, due to several interruptions, it was not possible to keep a continuous series of collections at each site in each year. Missing collections in the bi-weekly series were replaced with samples collected in the following week or when necessary, during the previous week.

2.3. Bee collections

Solo brand PS6-0099 plastic bowls (6 oz. capacity) were painted in three colours (fluorescent blue Krylon paint brand #3109, fluorescent yellow #3104 and white) to create pan traps. These were filled to two-thirds with a solution of water and Dawn brand blue soap, used as a surfactant. Thirty pan traps (10 of each colour) were set out in rotating colours along pre-established transect patterns. Pan traps were set before 9:00h and recovered after 15:00h.

Different transect patterns were used in different years as the Bee Inventory Plot Protocol was adjusted depending on site dimensions (LeBuhn *et al.*, 2003). Transects were set by different collectors over the years. In 2003, A. Rutgers-Kelly and B. Baker set the X140 pattern in BrockNW and BrockS and the H-like pattern in Pond and St. Davids (Table 1). In order to set the X140 pattern, two 140 m transects were established, forming an X-like pattern, where 15 pan traps were placed on each transect with a 10 m distance in between. The H-like pattern consisted of two parallel transects of un-equal length (70 m and 80 m) separated by a 140 m transect perpendicular to both (M. Frampton, *pers. comm.*). E. Law and A. Ironside reproduced these settings in 2004, although in 2006 (when M. Frampton was the collector) the P140 pattern was selected for Pond and St. Davids. The P140 pattern consisted of two parallel 140 m transects which were separated by 20 m. In each of the two transects 15 pan traps were placed at a distance of 10 m in between. Finally in 2008 J. Vickruck set the X050 pattern in all the sites. The X050 pattern consisted of two 50 m transects forming an X-like pattern, in which 15 pan traps were placed at a distance of 3.3 m in between.

Table 1. The transect patterns used in this study throughout the flight seasons of 2003, 2004, 2006 and 2008. In the first column, the description of each transect pattern is shown accompanied by a diagram (not to scale). The second column describes the transect lengths (m). The next column shows the distance between pan traps (m), while the year(s) and the sites in which each pattern was used are shown in the fourth and fifth columns, respectively.

Transect Pattern	Transect length	Distance between pan traps	Year(s)	Sites
P140. Parallel transects 	140 m	10 m	2006	Pond St. Davids
X050. X-like pattern 	50 m	3.3 m	2008	Brock NW Brock S Pond St. Davids
X140. X-like pattern 	140 m	10 m	2003 2004 2006	BrockNW BrockS
H-like pattern 	80 m 140 m 70 m	10 m	2003 2004	Pond St. Davids

The transect patterns differed in length and shape (i.e. parallel, X- and H-like pattern) covering unequal areas, which might have resulted in differences in their specimen collection rates (sampling effort). Differences in sampling effort among transect patterns might influence annual estimates of bee abundance and diversity. To address this issue, the P140, X050 and X140 patterns were compared in the field in 2010 in order to measure potential differences in sampling effort. The results are presented in Appendix I. No significant differences were detected in species richness or in the number of bees collected per date or per pan trap colour among the P140, X050 and X140 patterns.

2.4. Bee handling and identification

At the end of each day of collection, the contents of each pan trap were transferred into 750 ml plastic containers labelled with the date and the location. Upon arrival at the laboratory, insects were rinsed with water and temporarily stored in BD Biosciences brand 50 ml Falcon tubes containing 70% ethanol, until sorting. Bee specimens were sorted from other arthropods, then pinned and labelled indicating the site, the date and the method of collection.

For the year 2003, specimens had been previously identified to genus and species (Richards *et al.*, 2011). For specimens collected in 2004, 2006 and 2008, I carried out the identification to genus and, whenever possible, to species level. However, specimens that required high expertise (*Andrena*, *L. (Dialictus)* and *Nomada*) were only identified to genus. As a result, the species richness of the bee community for 2004, 2006, and 2008 should be regarded as underestimated.

Identifications were carried out with the help of a Meyer Instruments brand Leica-MS5 stereomicroscope. Most specimens were identified using the identification guides of Laverty and Harder (1988), Michener *et al.* (1994) and Mitchell (1960, 1962) in addition to the online guide Discover Life for identification of bees of eastern North America (http://www.discoverlife.org/mp/20q). The collection of Professor Richards at Brock University was also reviewed as a reference. Specimen records were organised by years (i.e. 2003, 2004, 2006 and 2008) into different databases using the computer program Microsoft ® Excel 2007.

2.5. Ecological traits of the bee community

The different strategies that species have with respect to the selection and diversity of nesting resources and habits allowed for the classification of this bee community in the following nesting guilds: miner, mason, small cavity nesters, carpenter, large cavity nesters and kleptoparasitic. Information on the nesting guilds of this bee community was obtained from Barrows (1973), Cane *et al.* (2007), Eickwort (1975), Laverty and Harder (1988), Michener (2000), Murray *et al.* (2009), Potts *et al.* (2005), Richards *et al.* (2011) and Sheffield *et al.* (2003, 2008). Social habits were classified as solitary, social or parasitic based on the classification proposed by Michener (1969, 2000). Information on social habits was obtained from Michener (1969), Laverty and Harder (1998) and Richards *et al.* (2011). Species of this bee community were considered as univoltine, bivoltine or multivoltine if they produced one, two or more generations per year, respectively. Information on voltinism of the species of the bee community was

obtained from Brady *et al.* (2006), Danforth (2002), Laverty and Harder (1998), Schwarz *et al.* (2007), and Thorp and Leong (1998).

2.6. The phenology of the bee community

Annual variation in phenology was analysed as differences in the proportion of individuals of each genus, collected per week in each of the four years studied. In addition, variation in the timing of high bee activity for the abundant species was also compared among years.

2.7. Abundance of the bee community

Bee abundance was considered in terms of the number of bees collected according to genus, species, site and disturbance level. The number of bees of each genus (or species) was log-transformed after a half-unit was added to their abundance, in order to ensure that represented values were all greater than zero. All specimens of the dataset of four years were used for genera but not for species. Specimens belonging to *Andrena, L. (Dialictus)* and *Nomada* were excluded from the species rank abundance distribution.

The study of Richards *et al.* (2011) was used to define bee genera and species as abundant, common or rare. Genera or species were regarded as abundant when they represented about 5% or more of the total number of individuals. The common genera and species ranged between this level and a cut-off point of ≥4 bees. In turn, this cut-off point separated common from rare genera and species (<4 bees) based on the minimum number of bees that would be necessary to occupy the four sites of this study. A data subset was selected from bees collected bi-weekly in 2003 using pan traps that had been

deployed in seven field sites. The rank abundance distribution of genus and species was graphically represented, and in the case of the latter the aforementioned taxa were excluded. The genus or species cumulative abundance was also plotted and helped to identify the proportional representation of each group. Subsequently, the same procedure was also used to define the genus and species groups of this study, and the results of both studies were compared.

2.8. Annual variation in abundance

The annual pattern of variation was investigated for the number of bees collected according to genera and species and according to site and disturbance level. The inter-annual variation of genus and species abundance was graphically represented by using the rank abundance distribution of the year 2003 as a reference.

2.9. The diversity of the bee community

The diversity of the bee community was measured as the number of genera and the species richness. In addition, diversity was also assessed in terms of the proportions of bees according to family, nesting guild, social habit, and voltinism.

2.10. Annual variation in diversity

The analysis of annual variation patterns in diversity required first estimating the total diversity present at the sites for the overall four years studied and for each year. Subsequently, I investigated whether generic and species richness in addition to genus and species turnover varied annually and whether proportional representation of genera

and species varied among years. The observed annual variation patterns were also analysed according to family, nesting guild, social habit and voltinism.

Bees collected bi-weekly at the four sites over the four years studied were used to estimate the annual change in the total diversity of the bee community. This was important given that not all the genera or species present at the sites could be collected each year. All specimens were used for the estimation of generic richness; *Andrena*, *L. (Dialictus)* and *Nomada* bees were excluded from the species richness estimation.

Rarefaction curves were constructed to compare generic and species richness among years using the program Rarefaction Calculator (Krebs and Brzustowski, 2000). The genus and species datasets (for each year and the four years studied) were compared at the size of the smallest sample, which was for the year 2008 (Brewer and Williamson, 1994). These curves also provided information about whether the sample size was sufficient to have collected the total genera and species present over the four years studied. To calculate the rarefaction curves individuals were randomly re-sampled without replacement, representing the average number of genera (or species) collected in 1, 2 ... n individuals (Gotelli and Colwell, 2001).

The variation in abundance ranks of genera and species was studied among years. I hypothesised that the ranks of the most abundant genera and species were more stable than the ranks of their rarer counterparts. For this purpose, the 2003 ranks were compared to the subsequent years. For each year, ranks were assigned in a serial manner starting from the most abundant and finishing with the rarest genus or species. In case of a tie among abundances, the mean rank was assigned to all the tying genera or species.

Specimens belonging to *Andrena, L. (Dialictus)* and *Nomada* were excluded from the species comparisons.

2.11. Statistical analysis

2.11.1. Tests for normality

Normality was assessed using the procedure Univariate in SAS version 9.2. The Kolmogorov-Smirnov analysis was performed to test the null hypothesis that a variable followed a normal distribution. A transformation was applied when the variable did not follow a normal distribution as indicated by Fowler *et al.* (1998), Wolda and Marek (1994), and Zuur *et al.* (2007). When normality assumptions were not met for ANCOVA and regression analyses, the variable was log-transformed. In this case, a half unit was added to all the values of the variable when zeros were present as suggested by Wolda and Marek (1994). Alternatively, when deviation from normality was not corrected by using the log-transformation, the variable was ranked using the procedure Rank in SAS v. 9.2. This procedure has been recommended by Conover (1999) and Conover and Iman (1981, 1982) because of its robustness and power. Conover and Iman (1981, 1982) reported that using ranked variables for regression analyses and ANCOVA tests reduced the Type I error probability and gained power in relation to parametric analyses.

2.11.2. Data analysis of the phenology

The phenology analysis tested whether the number of bees collected in spring (Weeks 1 to 11) differed significantly from the number of bees collected in summer (Weeks 13 to 23). Therefore, a χ^2 goodness of fit test was performed for testing the null

hypothesis that the number of bees collected over the four pooled flight seasons had an even distribution. The same analysis was also performed for testing the annual variation pattern in the phenology of the overall community and the abundant species.

2.11.3. Data analysis of abundance among sites

Chi-square goodness of fit tests were performed for testing the null hypotheses that bees were evenly distributed among sites and disturbance levels.

2.11.4. Data analysis of annual variation in abundance

Two ANCOVA analyses were performed (using the procedure GLM in SAS v. 9.2) in order to test for significant relationships between the number of bees collected per genus (or species) and year. The variable 'year' was treated as continuous while 'genus' (or 'species') was treated as categorical. The response variables number of bees and log (N + 0.5) were not normally distributed, hence the analysis was done on ranked variables. In addition, in order to detect annual variation patterns in abundance for each species, a regression analysis was performed for the number of bees collected per year from the four sites. When normality assumptions for the number of bees and log (N + 0.5) were not met, the analysis was then performed on the ranked variable.

The annual variation pattern of the proportion of bees collected according to site was analysed by performing a χ^2 goodness of fit test. In addition, a χ^2 goodness of fit test was also performed to analyse significant differences in the proportion of bees collected according to disturbance level.

2.11.5. Data analysis of diversity

Separate χ^2 goodness of fit tests were performed for testing whether the proportion of bees according to family, nesting guild, social habit and voltinism was evenly distributed.

2.11.6. Tests for estimated diversity variation among years

The Abundance-based Coverage Estimator (ACE) and the classical Chao-1 estimator were used to assess the total generic and species richness present annually, choosing the higher of the two estimators (Chao, 1984; Chao, 2004; Chao and Lee, 1992). Both estimations were performed using EstimateS (Colwell, 2009) with 50 randomisations based on the dataset of four years and subsets for each year. As suggested by Colwell (2009), the bias-corrected Chao-1 was used when genera with only 2 individuals (doubletons) were absent. It was also used when there was just one doubleton species since it was found to be more accurate than the classical version.

2.11.7. Tests for annual differences in the number of genera and species richness

Randomisation analyses were performed in order to test the null hypotheses stating that the number of genera and the species richness did not vary among years. Richardson and Richards (2008) designed the randomisation analysis used in the current study. These authors have already shown the robustness of this randomisation analysis to test the null hypothesis that no differences in the species richness will be found among samples. The first step prior to the analysis was pooling the bee specimens collected in each of the four samples (i.e. the years 2003, 2004, 2006 and 2008). Subsequently, the

computer program randomly re-assigned each bee to each year respecting both the number of bees that each genus (or species) had and the number of bees collected in each of the years. This process was repeated 10,000 times and as a result, the program generated a frequency distribution of the expected number of genera or species for each year. The observed values of the number of genera or species were then contrasted to the 95% confidence intervals of the frequency distribution in order to identify significant differences among the four years studied. The randomisation analysis of genera was performed for all the specimens collected during the four years studied, although specimens belonging to *Andrena, L. (Dialictus)* and *Nomada* were excluded from the species randomisation analysis.

2.11.8. Tests for the annual turnover of genera and species

To test the hypothesis that annual genus and species turnover would increase with years, the change in genus and species similarity was analysed over the four years studied. Variation in composition and relative abundance of genera and species were compared among pairs of years using an Abundance-based Jaccard Index (J_{abd}). This index also accounted for the effect of shared rare taxa that might not be detected in smaller samples (Chao *et al.*, 2005). The J_{abd} index has proven to be less biased than its classic version, demonstrating its accuracy for samples differing in size, sampling effort or having numerous rare taxa (Chao *et al.*, 2005; Chao *et al.*, 2006). The computer program EstimateS was used to calculate the J_{abd} index. Values ranged between 0 for total dissimilarity to 1 for complete similarity. The J_{abd} index was calculated as:

$$\hat{J}_{abd} = \frac{\hat{U}\hat{V}}{\hat{U} + \hat{V} - \hat{U}\hat{V}}$$

$\hat{U}$ = Total relative abundances of individuals in the year 1 belonging to the shared species (adjusted for the not detected shared species)

$\hat{V}$ = Total relative abundance of individuals in the year 2 belonging to the shared species (adjusted for the not detected shared species)

2.11.9. Additional data analysis for annual variation in diversity

Annual variation in the proportions of bees according to family, nesting guild, social habit and voltinism were tested by performing χ^2 tests of goodness of fit.

3. RESULTS

3.1. General description of the bee community

A total of 8139 bee specimens was available in the four pooled years of bi-weekly collections, 2003, 2004, 2006 and 2008 (Table 2). Specimens belonged to the 5 families (Halictidae, Megachilidae, Apidae, Colletidae and Andrenidae) typically found in eastern North America. The whole bee fauna collected consisted of 26 genera and sub-genera and at least 57 species (not including *Andrena, L. (Dialictus)* and *Nomada*). The most abundant genera of the bee community were *Augochlorella, Ceratina, L. (Dialictus), Halictus, Hylaeus*, and *Osmia.* The two most common species were *Augochlorella aurata* (family Halictidae) with 2745 individuals and *Osmia conjuncta* (family Megachilidae) with 1193 individuals. The following species were represented by only one specimen: *Hoplitis truncata, Lasioglossum (Evylaeus) macoupinense, Megachile inermis, Megachile mendica, Protandrena andrenoides, Osmia simillima*, and *Xylocopa virginica.* Please refer to Appendix II for information on bees sampled during the complete flight seasons of the four years studied.

3.2. The phenology of the bee community

In terms of its phenology the bee community presented three peaks of high foraging activity (Fig. 2). The first peak occurred in spring (Week 5), followed by a decline in foraging activity by the summer solstice, the time when days begin to shorten (Week 11). Two peaks in summer, occurring in Week 13 and Week 19, represent the peak of worker brood production and emergence of reproductive brood of eusocial species. The most active part of the bee season took place in spring (Weeks 1 to 11),

Table 2. Number of bees per species collected, through the use of pan traps, in 2003, 2004, 2006 and 2008. Sampling frequency was bi-weekly at four sites (BrockNW, BrockS, Pond and St. Davids) of the Niagara Region. Species were denoted as *sp.* when complete identification to species level was not possible. Information on nesting guilds and social habits was obtained from: Barrows, 1973; Cane *et al.*, 2007; Eickwort, 1975; Grixti and Packer, 2006; Michener, 2000; Richards *et al.*, 2011 and Sheffield *et al.* 2003.

Family	Genus	Species	Nesting guild	Social habit	Voltinism	2003	2004	2006	2008	Grand Total
Andrenidae	*Andrena*	*sp.*	Miner	Solitary	Univoltine	97	21	20	53	191
	Calliopsis	*andreniformis*	Miner	Solitary	Univoltine	4	1	2	0	7
	Protandrena	*andrenoides*	Miner	Solitary	Univoltine	1	0	0	0	1
Andrenidae Total						102	22	22	53	199
Apidae	*Anthophora*	*terminalis*	Carpenter	Solitary	Univoltine	1	0	1	0	2
	Apis	*mellifera*	Large cavities	Social	Multivoltine	16	8	16	14	54
	Bombus	*citrinus*	Kleptoparasitic	Kleptoparasitic		1	1	0	0	2
		fervidus	Larg cav./grass	Social	Bivoltine	0	2	4	3	9
		griseocollis	Large cavities	Social	Bivoltine	0	1	3	4	8
		impatiens	Large cavities	Social	Bivoltine	1	0	1	7	9
		mixtus	Large cavities	Social	Bivoltine	0	0	2	0	2
		rufocinctus	Large cavities	Social	Bivoltine	1	0	2	0	3
		sandersoni	Large cavities	Social	Bivoltine	0	0	3	0	3
		vagans	Large cavities	Social	Bivoltine	0	2	1	0	3
	Ceratina	*calcarata*	Carpenter	Solitary	Univoltine	183	53	53	64	353
		dupla/mikmaqi	Carpenter	Solitary	Univoltine	215	70	40	121	446
		strenua	Carpenter	Solitary	Univoltine	2	0	0	0	2
	Melissodes	*desponsa*	Miner	Solitary	Univoltine	1	0	1	1	2

Table 2 (Continued)

Family	Genus	Species	Nesting guild	Social habit	Voltinism	2003	2004	2006	2008	Grand Total
Apidae	*Nomada*	*sp.*	Kleptoparasitic	Kleptoparasitic		3	0	4	9	16
	Triepeolus	*simplex*	Kleptoparasitic	Kleptoparasitic		0	1	2	0	3
	Xylocopa	*virginica*	Carpenter	Social	Univoltine	1	0	0	0	1
Apidae Total						425	138	132	223	918
Colletidae	*Hylaeus*	*affinis*	Small cavities	Solitary	Bivoltine	109	30	340	47	526
		affinis/modestus	Small cavities	Solitary	Bivoltine	27	0	4	12	43
		annulatus	Small cavities	Solitary	Bivoltine	3	0	4	0	7
		mesillae	Small cavities	Solitary	Bivoltine	7	2	0	5	14
		modestus	Small cavities	Solitary	Bivoltine	8	4	4	0	16
		sp.	Small cavities	Solitary	Bivoltine	0	0	0	1	1
Colletidae Total						154	36	352	65	607
Halictidae	*Agapostemon*	*virescens*	Miner	Social	Univoltine	13	4	10	8	35
	Augochlora	*pura*	Carpenter	Solitary	Univoltine	5	1	0	0	6
	Augochlorella	*aurata*	Miner	Social	Bivoltine	922	715	791	317	2745
	Halictus	*confusus*	Miner	Social	Bivoltine	169	105	138	44	456
		ligatus	Miner	Social	Bivoltine	166	171	303	17	657
		rubicundus	Miner	Social	Bivoltine	11	10	26	8	55
	L. (Dialictus)	*sp.*	Miner			293	197	47	94	631
	L. (Evylaeus)	*cinctipes*	Miner		Bivoltine	5	0	1	0	6
		macoupinense	Miner	Social		0	0	0	1	1
	Lasioglossum	*coriaceum*	Miner	Solitary	Univoltine	7	4	1	0	12

Table 2 (Continued)

Family	Genus	Species	Nesting guild	Social habit	Voltinism	2003	2004	2006	2008	Grand Total
Halictidae	*Lasioglossum*	*leucozonium*	Miner	Solitary	Univoltine	18	8	12	8	46
		zonulum	Miner	Solitary	Univoltine	37	5	2	0	44
		sp. damaged	Miner	Solitary	Univoltine	0	1	0	0	1
Halictidae Total						1646	1221	1331	497	4695
Megachilidae	*Anthidiellum*	*notatum*	Mason	Solitary	Univoltine	4	0	0	0	4
	Anthidium	*manicatum*	Mason	Solitary	Univoltine	20	3	9	0	32
	Coelioxys	*rufitarsis*	Kleptoparasitic	Kleptoparasitic		0	1	7	0	8
	Hoplitis	*pilosifrons*	Mason	Solitary	Univoltine	27	5	15	26	73
		producta	Mason	Solitary	Univoltine	4	3	6	8	21
		spoliata	Mason	Solitary	Univoltine	5	0	3	0	8
		truncata	Mason	Solitary	Univoltine	0	1	0	0	1
	Megachile	*brevis*	Mason	Solitary	Univoltine	16	13	39	2	70
		centuncularis	Mason	Solitary	Univoltine	0	0	1	1	2
		inermis	Carpenter	Solitary	Univoltine	0	0	1	0	1
		latimanus	Miner	Solitary	Univoltine	1	2	6	1	10
		mendica	Mason	Solitary	Univoltine	1	0	0	0	1
		montivaga		Solitary	Univoltine	0	0	2	0	2
		relativa	Mason	Solitary	Univoltine	0	0	2	0	2
		rotundata	Mason	Solitary	Univoltine	27	1	2	0	30
		texana	Mason	Solitary	Univoltine	3	0	4	4	11
		sp.		Solitary	Univoltine	0	0	1	0	1
	Osmia	*albiventris*	Mason	Solitary	Univoltine	0	6	15	30	51

Table 2 (Continued)

Family	Genus	Species	Nesting guild	Social habit	Voltinism	2003	2004	2006	2008	Grand Total
Megachilidae	*Osmia*	*atriventris*	Mason	Solitary	Univoltine	14	3	25	11	53
		conjuncta	Mason (shells)	Solitary	Univoltine	385	133	331	344	1193
		inspergens	Mason	Solitary	Univoltine	0	0	1	9	10
		lignaria	Mason	Solitary	Univoltine	1	0	1	1	3
		pumila	Mason	Solitary	Univoltine	47	7	28	33	115
		simillima	Mason	Solitary	Univoltine	1	0	0	0	1
		sp.	Mason	Solitary	Univoltine	0	1	0	6	7
	Stelis	*lateralis*	Kleptoparasitic	Kleptoparasitic		5	3	2	0	10
Megachilidae Total						561	182	501	476	1720
Grand Total						2888	1599	2338	1314	8139

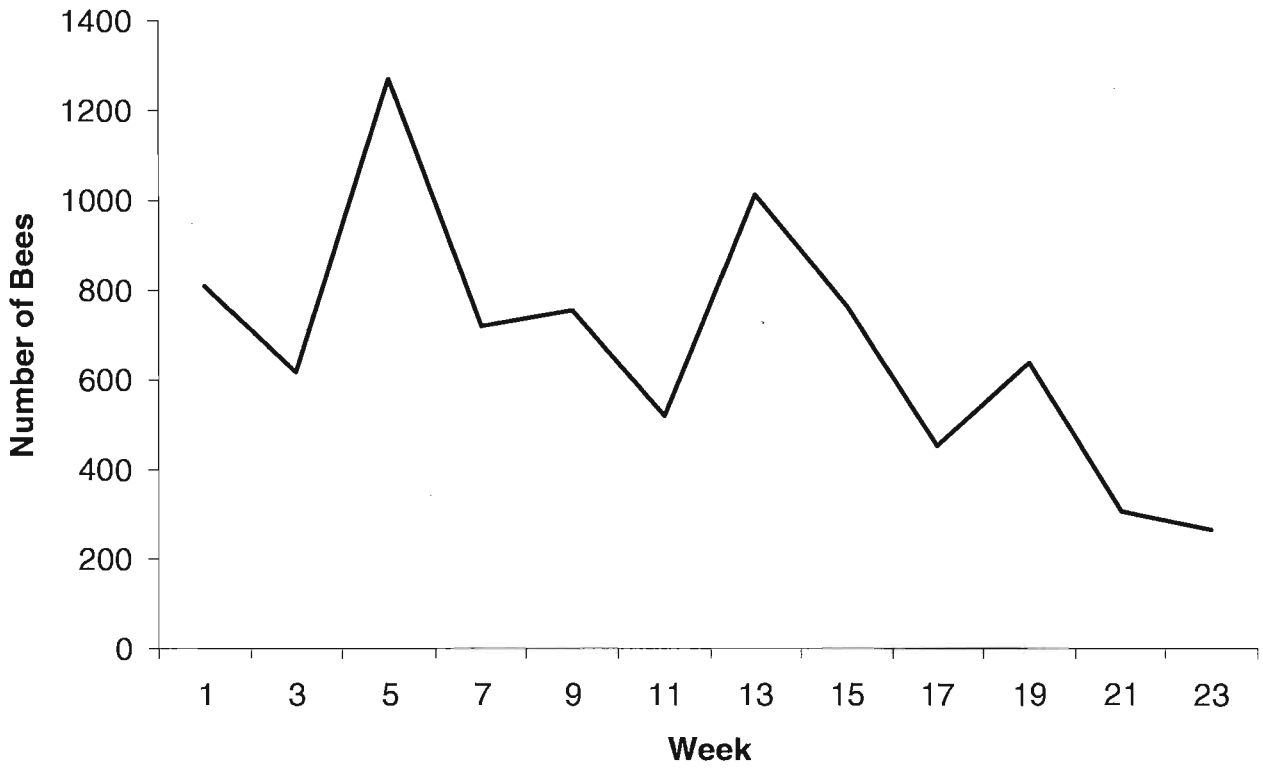


Fig. 2. Phenology of the bee community. The collections of four years were pooled in a bi-weekly basis. The bee community presented one peak in spring centred on Week 5 of high foundress bee foraging activity and two peaks in summer centred on Week 13 and Week 19 (corresponding to the worker and reproductive broods of bivoltine species, respectively). During Week 11 there was a decline of bee community activity which corresponded to the summer solstice.

before the summer solstice when the number of bees collected was higher than in summer (Weeks 13 to 23) (goodness of fit test: $\chi^2 = 1305.4$, d.f. = 11, $p<<0.001$).

The phenology of the abundant species and the overall bee community varied annually (Fig. 3, Table 3; goodness of fit tests: $\chi^2 = 2070.2$, d.f. = 33, $p<<0.001$; $\chi^2 = 2281.7$, d.f. = 33, $p<<0.001$, respectively). In both cases the 2003 and 2006 seasons were generally longer and more advanced, with spring and summer high flight activity being detected earlier than in 2004 and 2008. Except for 2003, more bees were captured in spring than in summer, with the lowest number of bees collected during the summer of 2008. In 2006, the bivoltine *A. aurata* and *H. ligatus*, occurring in Week 1, had one of the most advanced seasons, while for the univoltine *Ceratina dupla/mikmaqi* and *C. calcarata*, occurring in Week 5, it was the most delayed season.

3.3. Abundance of the bee community

In the 2003 survey, the six most abundant genera represented 90% of individuals (Fig. 4). The next genus group represented almost 10% of the bees, while the genera with fewer than four bees represented less than 0.1% of individuals. This allowed the genus classification of the current study into the following three groups: abundant, common and rare genera. Over the four pooled study years the same abundant genera represented almost 91% of the bee community (Fig. 5). The common genera represented 9% of the bees, while the rare genera represented 0.1% of individuals. Between both surveys, the common and rare genus groups shared 19 genera, with only *Melissodes* changing from a common to a rare genus. Overall, genus composition remained quite stable between the two surveys and differences were only found among rare genera, with *Chelostoma*,

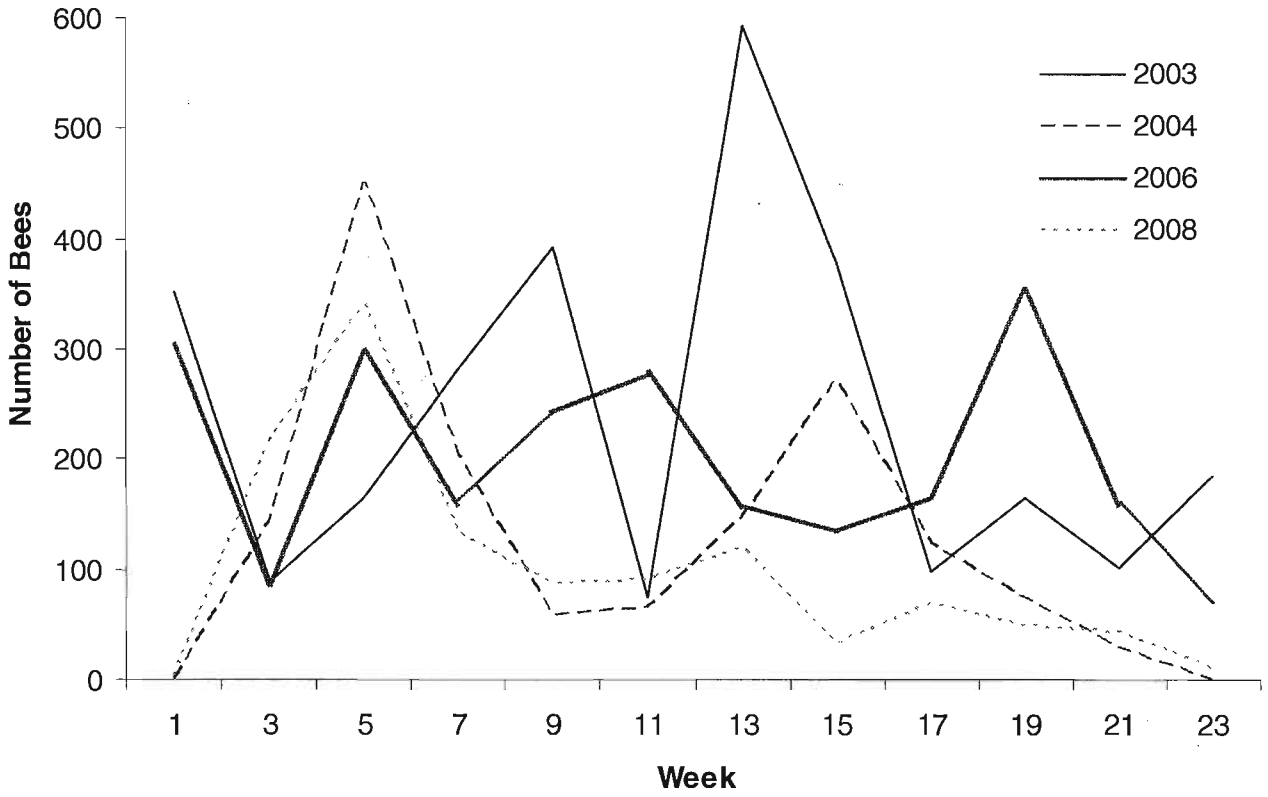


Fig. 3. Annual variation of the phenology of the bee community. This was calculated as the proportion of bees (of the overall bee community) collected per week in each of the four years studied.

Table 3. Inter-annual comparison of phenology for the abundant species. Bees were collected bi-weekly from the last week of April (Week 1) to the last week of September (Week 23). The summer solstice, occurring in Week 11, divided the bee season in spring and summer. Bivoltine and univoltine species were grouped separately and weeks of high bee abundance were marked in bold. For some species having a low abundance over the season, weeks representing a relatively high value were also marked.

		Week												
		1	**3**	**5**	**7**	**9**	**11**	**13**	**15**	**17**	**19**	**21**	**23**	
Bivoltine species	**Year**	**Spring**						**Summer**						**Total**
A. aurata	2003	21	13	**43**	**106**	**170**	7	**227**	**157**	21	**39**	24	**94**	922
	2004	0	20	**323**	**86**	18	12	**83**	**103**	**42**	**25**	3	0	715
	2006	**90**	**45**	**115**	16	20	**114**	**66**	**56**	36	**144**	**91**	**51**	844
	2008	0	**26**	**100**	**25**	12	8	**59**	18	14	12	**33**	1	308
H. affinis	2003	0	0	0	**7**	**6**	4	**24**	7	8	**32**	**17**	4	109
	2004	0	0	1	**5**	3	**4**	1	3	3	**7**	3	0	30
	2006	0	0	2	**21**	**114**	**35**	11	13	**61**	**68**	8	4	337
	2008	0	0	1	**9**	**17**	**15**	**7**	0	**6**	**9**	2	2	68
H. confusus	2003	2	0	2	4	5	3	**85**	**44**	8	7	3	4	167
	2004	0	2	0	**20**	3	**18**	**20**	**28**	9	5	0	0	105
	2006	0	0	4	6	**22**	**59**	**16**	8	7	**10**	0	0	132
	2008	0	**6**	2	1	0	**12**	**14**	0	4	0	0	2	41
H. ligatus	2003	0	0	0	**21**	**16**	0	**20**	**30**	8	12	11	**48**	166
	2004	0	2	**62**	**20**	2	1	**28**	**44**	6	3	3	0	171
	2006	**8**	**19**	**32**	**29**	0	**25**	**19**	**22**	**38**	**86**	**20**	8	306
	2008	0	0	**4**	0	0	0	**3**	2	**4**	2	2	0	17

Table 3 (Continued)

		Week												
		1	**3**	**5**	**7**	**9**	**11**	**13**	**15**	**17**	**19**	**21**	**23**	
Univoltine species	**Year**	**Spring**						**Summer**						**Total**
C. dupla/mikmaqi	2003	**56**	8	**26**	**52**	**42**	0	**5**	**11**	**6**	**8**	1	0	215
	2004	0	**12**	**14**	**12**	5	3	1	**10**	0	**7**	**6**	0	70
	2006	0	0	**10**	**10**	**15**	1	2	0	0	2	0	0	40
	2008	0	**26**	**23**	**26**	8	**13**	3	0	**11**	1	1	2	114
C. calcarata	2003	6	1	**33**	**16**	**43**	**15**	**15**	**16**	5	**16**	**14**	2	182
	2004	0	**5**	**7**	**7**	**7**	3	1	**8**	2	**11**	2	0	53
	2006	0	0	**5**	**14**	**28**	2	0	0	0	0	0	1	50
	2008	0	**6**	**6**	**11**	**15**	2	1	2	**7**	**7**	0	2	59
O. conjuncta	2003	**163**	**39**	**39**	**39**	**60**	10	**20**	8	2	0	0	0	380
	2004	0	**57**	**25**	**27**	6	4	6	8	0	0	0	0	133
	2006	**155**	7	**82**	**41**	**15**	2	**16**	0	1	0	**25**	0	344
	2008	4	**93**	**132**	**30**	14	12	8	0	0	0	0	0	293

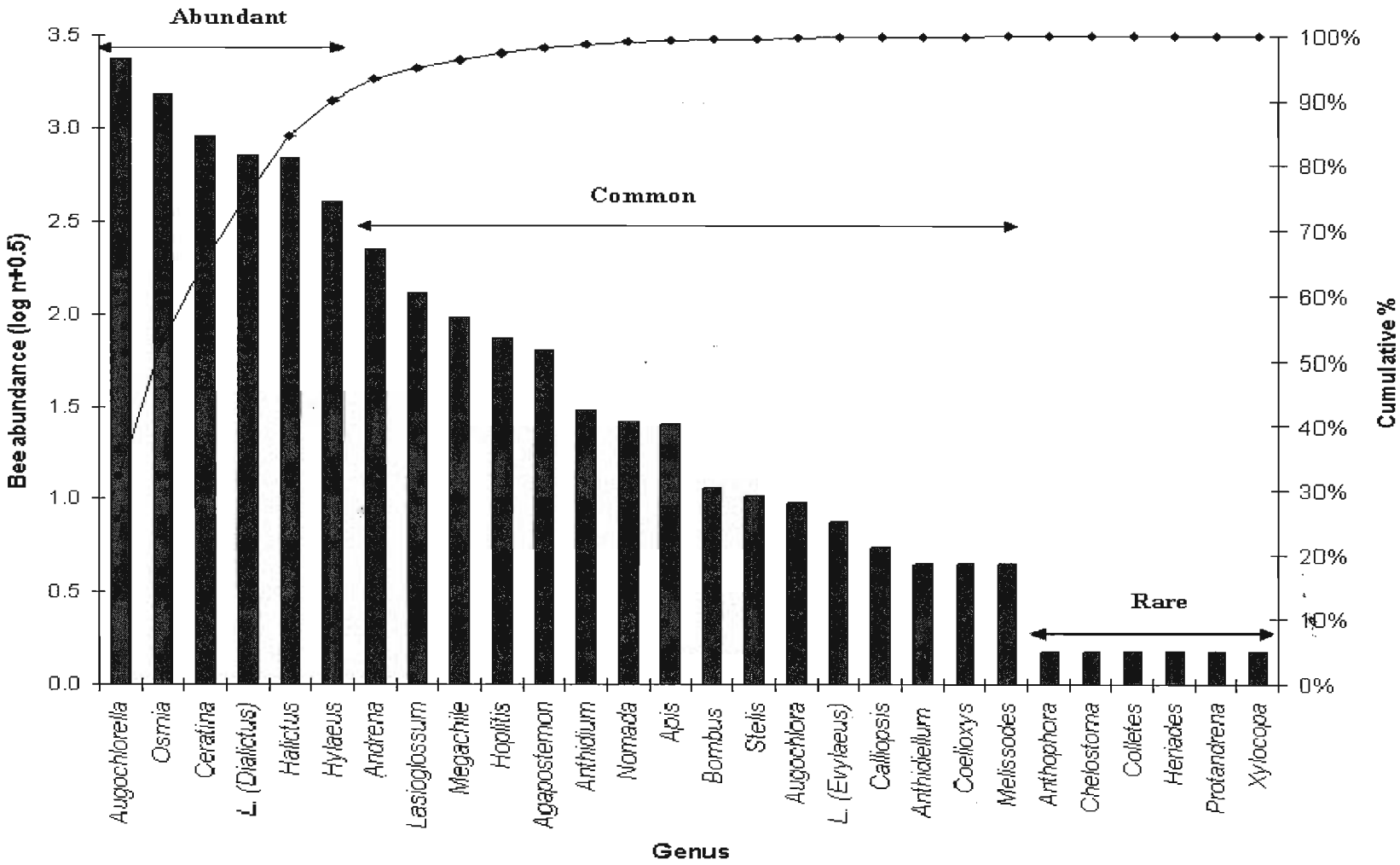


Fig. 4. Rank abundance distribution (bars) and cumulative abundance (diamonds) of genera for the bees collected bi-weekly in 2003 using pan traps at seven sites.

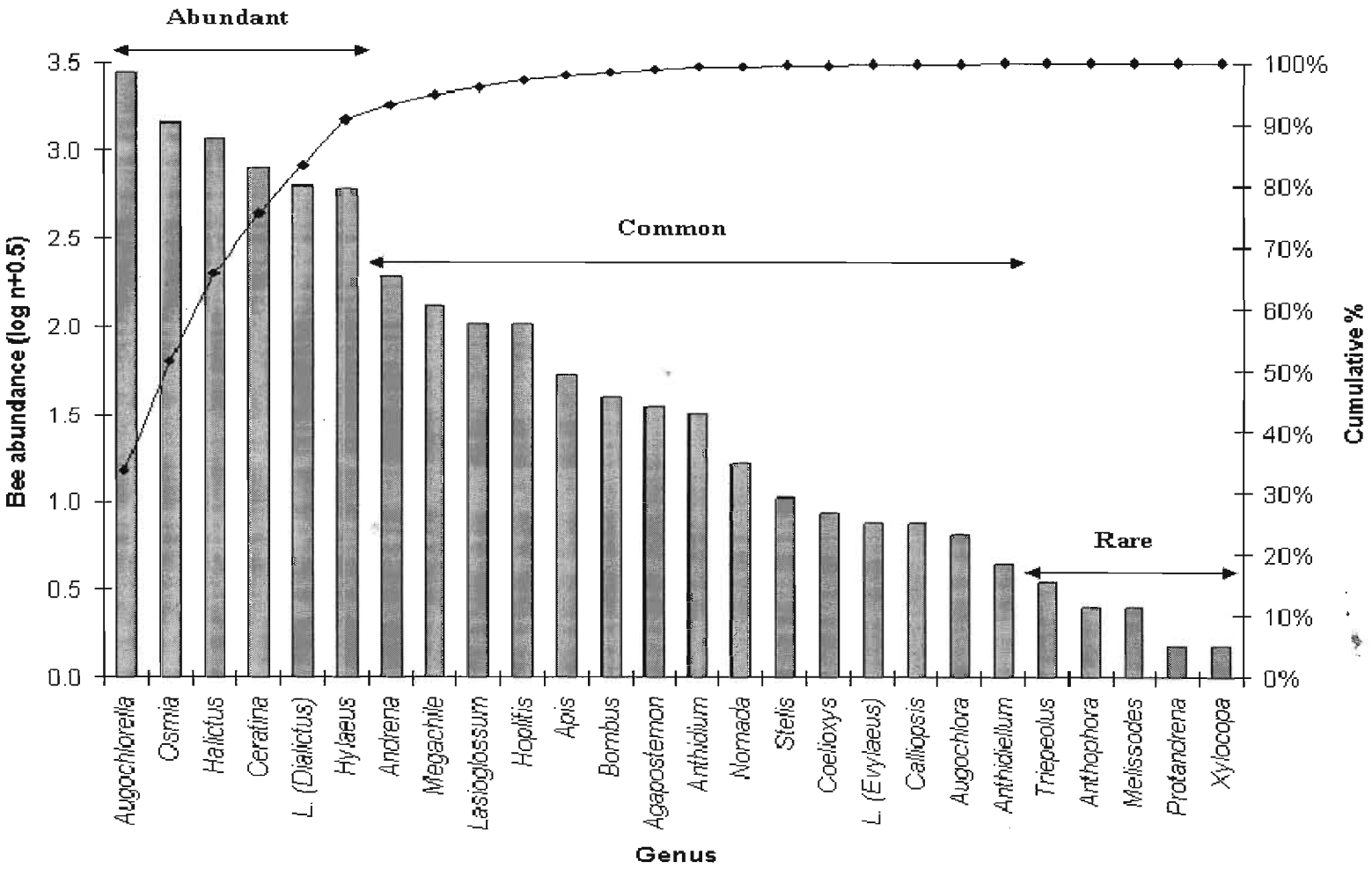


Fig. 5. Genera rank abundance distribution (bars) and cumulative abundance (diamonds) for bees pooled from 2003, 2004, 2006 and 2008. Individuals were collected bi-weekly using pan traps at four sites.

Colletes and *Heriades* unique to the 2003 study and *Triepeolus* unique to the four years studied.

In 2003, the seven most abundant species represented almost 89% of individuals: *A. aurata*, *O. conjuncta*, *C. dupla/mikmaqi*, *C. calcarata*, *H. ligatus*, *H. affinis* and *H. confusus* (Fig. 6). The 26 common species represented 11% of the bees, while species with fewer than four bees (rare) represented less than 1% of individuals. Over the four pooled study years the same seven most abundant species represented 88% of the bees (Fig. 7). The common species represented 11% of the individuals, while the rare species represented less than 1%. Between both surveys, thirty-five common and rare species remained in the same category; however twenty-one species were either collected in only one of the surveys or changed between the common and rare species categories (Table 4).

Individuals were not collected evenly among sites, which differed significantly in the number of bees collected (Fig. 8; goodness of fit test: $\chi^2 = 307.5$, d.f. = 3, $p<<0.001$). The highest number of bees was collected at BrockS (2502 bees) followed by BrockNW (2290 bees), Pond (1875 bees) and St. Davids (1472 bees). This suggests that previous disturbance influenced bee community abundance through its effect on the sites. Indeed, the number of bees collected at the low disturbance sites (BrockNW and BrockS) was significantly greater than in the high disturbance sites Pond and St. Davids (goodness of fit test: $\chi^2 = 256.5$, d.f. = 1, $p<<0.001$).

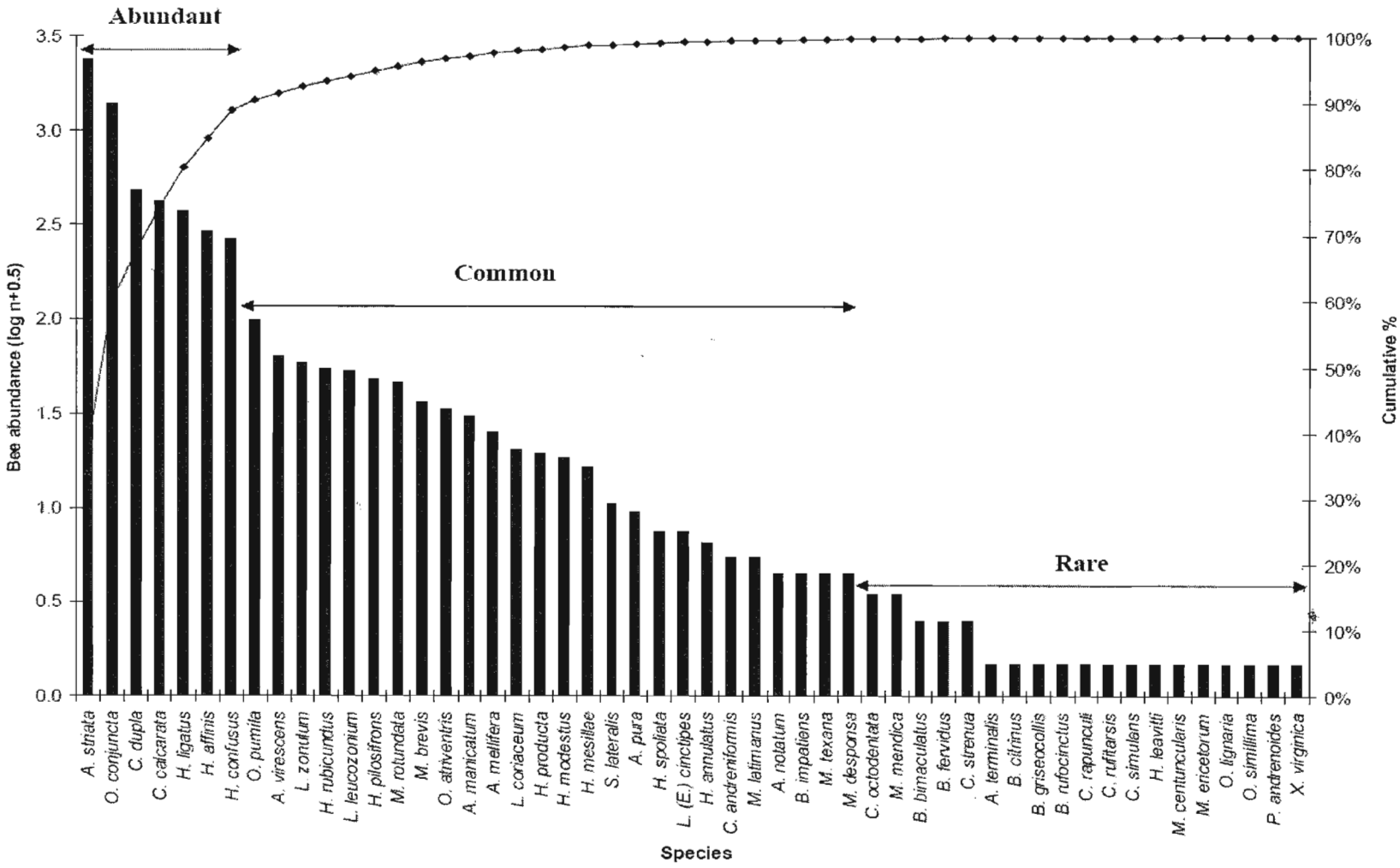


Fig. 6. Species rank abundance distribution (bars) and cumulative abundance (diamonds) for the bees collected throughout the complete 2003 season at seven sites.

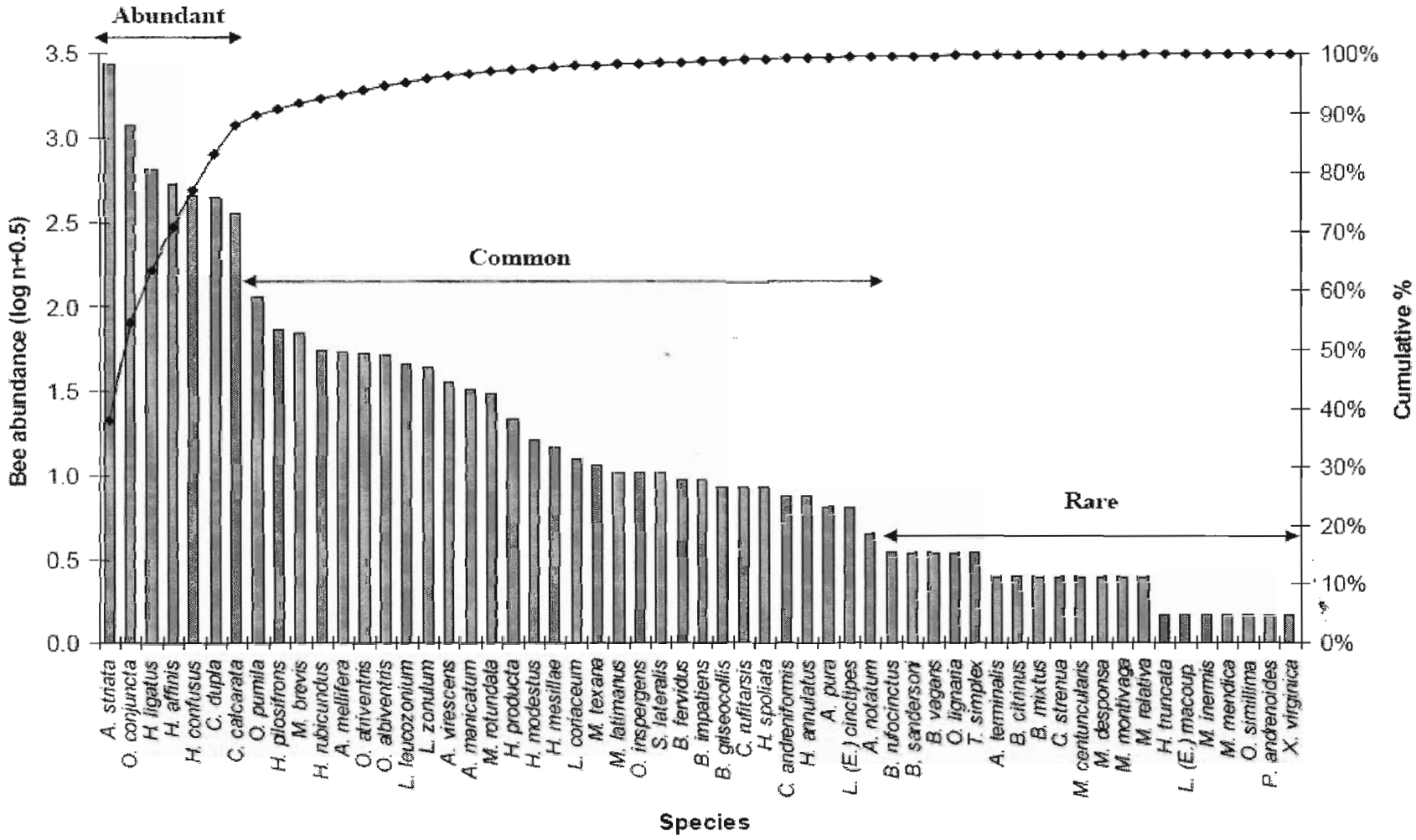


Fig. 7. Rank abundance distribution of species (bars) and cumulative abundance (diamonds) for bees of four pooled study years collected bi-weekly using pan traps at four sites.

Table 4. Species that changed between the common and rare species abundance categories or were collected in only one of the surveys.

	Species category	
Species	**2003 survey**	**Four-pooled years**
Bombus bimaculatus	Rare	-
Bombus fervidus	Rare	Common
Bombus griseocollis	Rare	Common
Bombus mixtus	-	Rare
Bombus sandersoni	-	Rare
Bombus vagans	-	Rare
Coelioxys octodentata	Rare	-
Coelioxys rapunculi	Rare	-
Coelioxys rufitarsis	Rare	Common
Colletes simulans	Rare	-
Heriades leavitti	Rare	-
Hoplitis truncata	-	Rare
Lasioglossum (Evylaeus) macoupinense	-	Rare
Melissodes desponsa	Common	Rare
Megachile ericetorum	Rare	-
Megachile inermis	-	Rare
Megachile montivaga	-	Rare
Megachile relativa	-	Rare
Osmia albiventris	-	Common
Osmia inspergens	-	Common
Triepeolus simplex	-	Rare

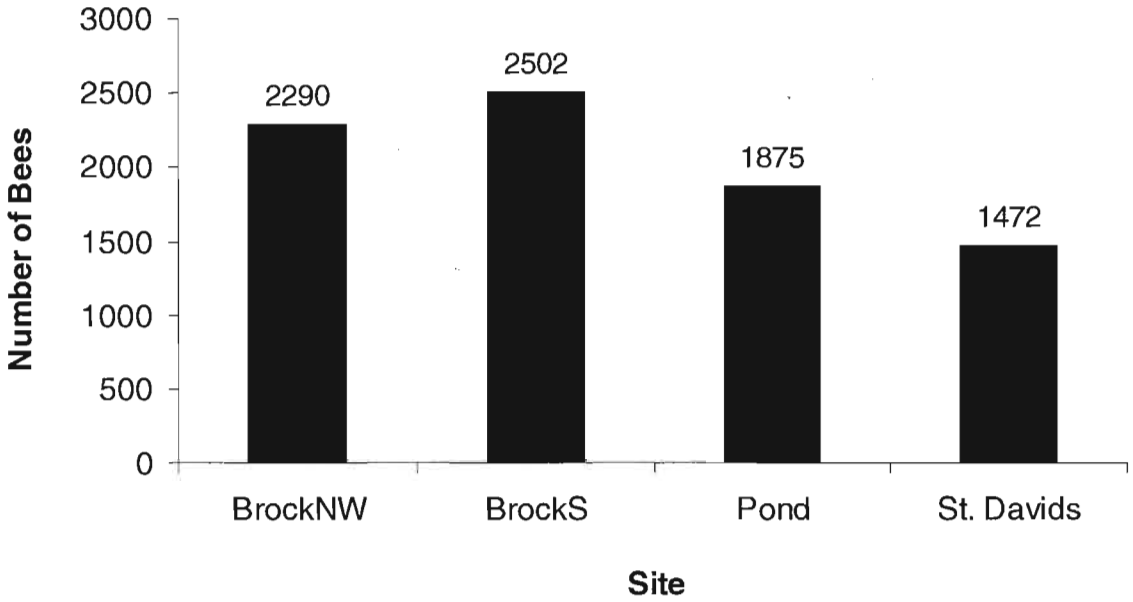


Fig. 8. Distribution of the number of bees among the study sites for the total of the four years studied. Both BrockS and BrockNW sites had a higher number of bees than Pond and St. Davids.

3.4. Annual variation in abundance

This bee community was characterised by annual variation in genus and species abundance (Figs. 9, 10). Bees of the six abundant genera in addition to the six more common genera (*Agapostemon*, *Andrena*, *Apis*, *Hoplitis*, *Lasioglossum* and *Megachile*) consistently occurred over the four years studied and rarely changed among abundance categories. The exceptions were two abundant genera that became common in one of the study years: *Hylaeus* in 2004, with 36 bees, and *L. (Dialictus)* in 2006, with 47 bees. However, the remaining common and rare genera more frequently changed categories and, with the exception of *Bombus*, were not collected in at least one study year. In terms of species abundance, the seven abundant and the following of the common species (*A. mellifera*, *A. virescens*, *H. rubicundus*, *H. pilosifrons*, *L. leucozonium* and *O. pumila*) were consistently collected over the four years studied, generally remaining in the same abundance categories. Only three abundant species became common in one of the study years: *H. affinis* in 2004 with 30 bees, and *C. calcarata* and *C. dupla/mikmaqi* in 2006, with 53 and 40 bees, respectively. However, the remaining common and rare species were variably collected, with the exception of *H. producta*, *Megachile brevis* and *M. latimanus*, were also absent from collections in at least one study year.

The number of bees collected varied from year to year, with 2888 bees in 2003, 1599 bees in 2004, 2338 bees in 2006 and 1314 bees in 2008. Annual patterns were also observed when both the number of bees collected per genus and species were considered. In the first case, normality was tested for the number of bees per genus and its log-transformation (Kolmogorov-Smirnov: $D = 0.33$, $p<0.010$; $D = 0.12$, $p<0.010$, respectively), and given that normality was not achieved, the former variable was ranked.

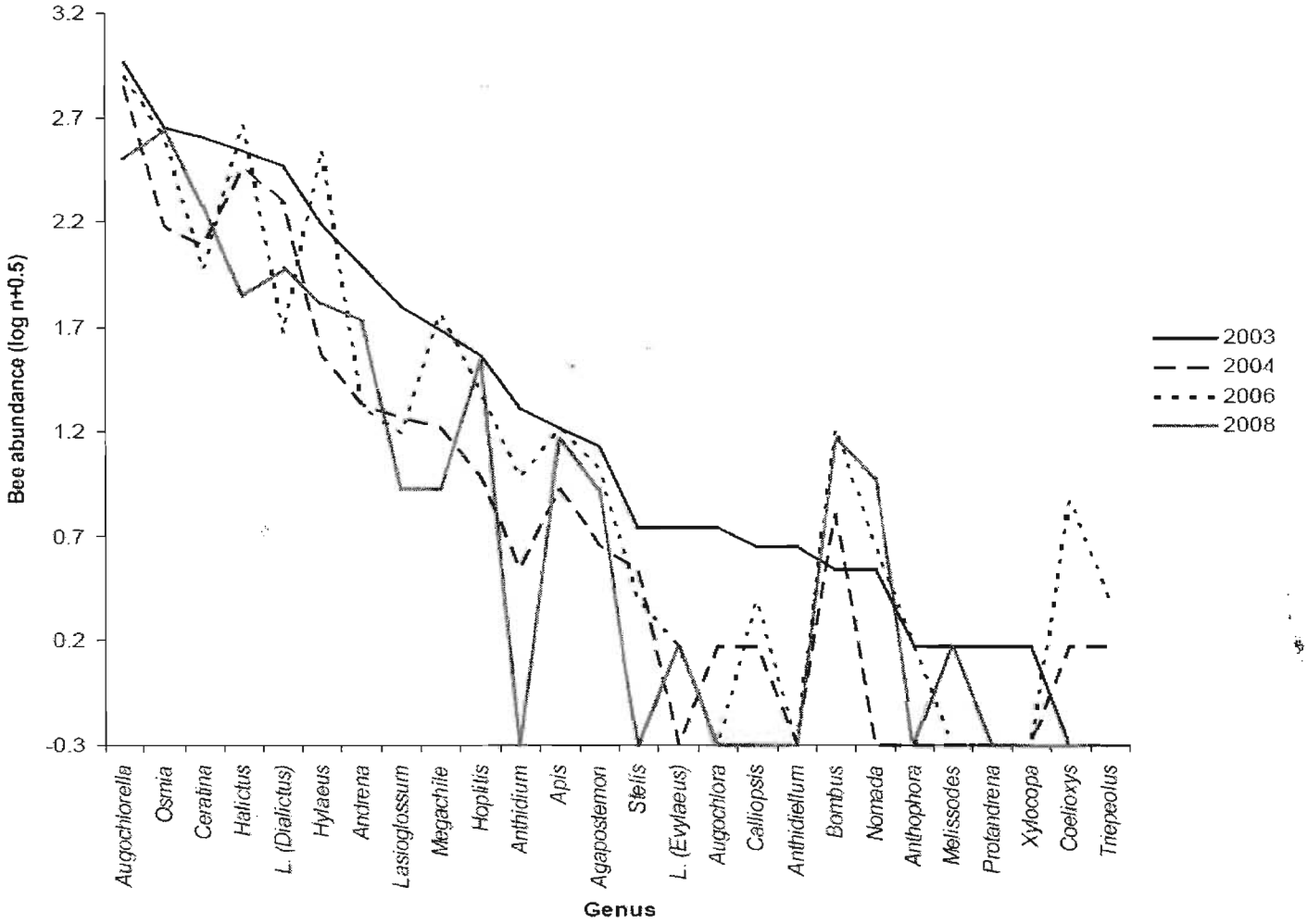


Fig. 9. Variation in genus abundance in the bee seasons of 2003, 2004, 2006 and 2008. The rank abundance distribution of the year 2003 was used as a reference for the subsequent years.

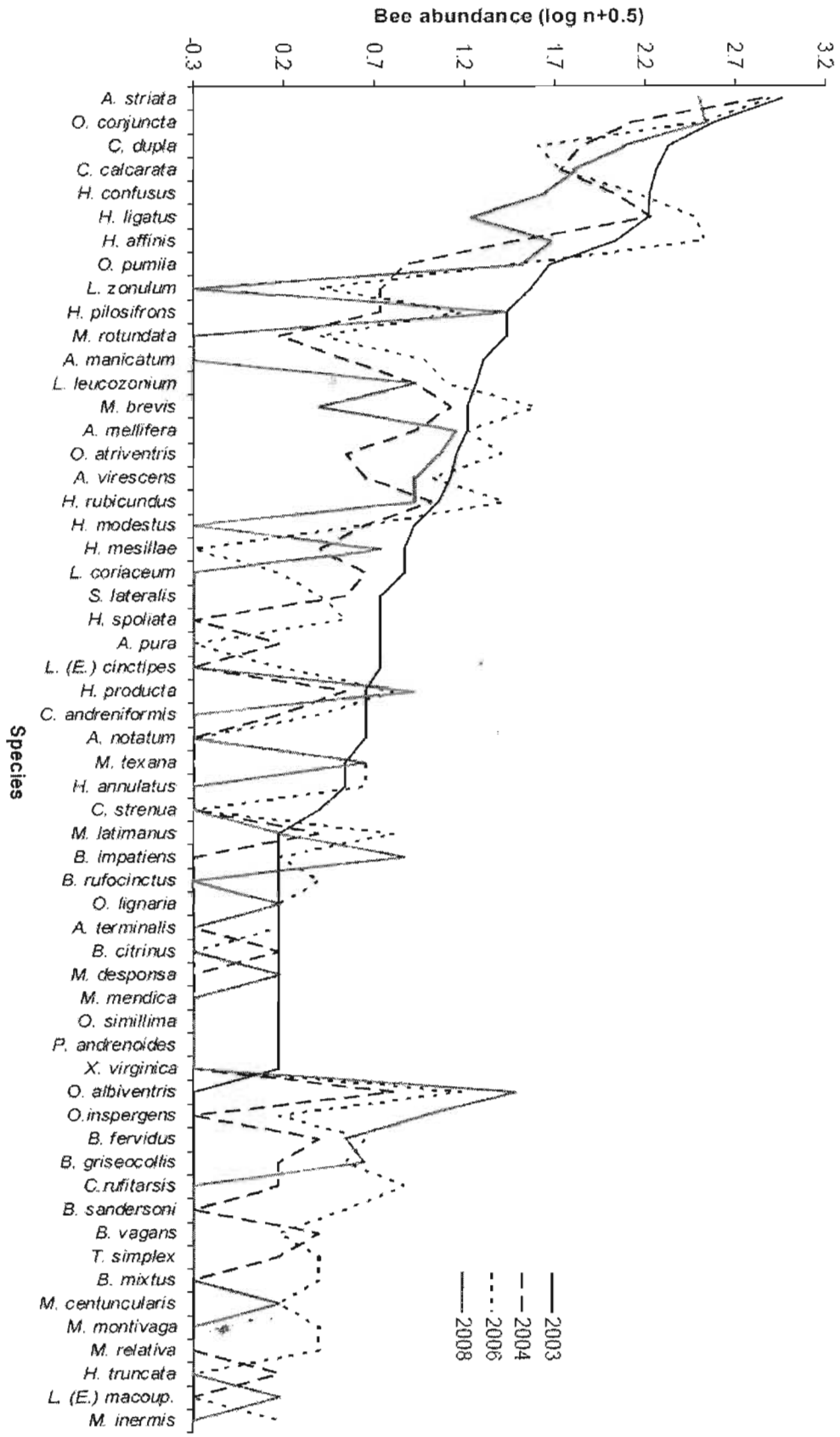


Fig. 10. Variation in species abundance in the bee seasons of the four years studied (2003, 2004, 2006 and 2008). The rank abundance distribution of the year 2003 was used a reference.

Subsequently, an ANCOVA test detected a significant relationship between the number of bees collected per genus and per year (Table 5). The effect of year was quite significant, which was the consequence of the year-to-year variation in genus abundance. In addition, the effect of genus was also significant although no significant year-genus interaction was detected. Similarly, normality was tested for both the number of bees per species and its log-transformation (Kolmogorov-Smirnov: $D = 0.39$, $p<0.010$; $D = 0.18$, $p<0.010$, respectively), and since normality was not achieved the former variable was ranked. The ANCOVA test detected a significant linear relationship between the number of bees collected per species and per year (Table 6). The effect of year was significant reflecting annual variation in the number of bees collected per species. In addition, the effect of species and the year-species interaction were also significant.

For each species, the number of bees collected per year from the four sites was analysed by performing a regression analysis. A significant regression was only found in eleven species (Table 7). Among these *H. confusus* was the only abundant species, while the remaining species (*A. pura*, *B. fervidus*, *B. griseocollis, B. impatiens*, *H. modestus*, *L. coriaceum*, *L. zonulum*, *M. rotundata*, *O. inspergens*, and *S. lateralis*) were common or rare and were not present in at least one year. In 2003, *B. fervidus*, *B. griseocollis* and *O. inspergens* were not collected, while in 2004, *B. impatiens* and also *O. inspergens* were absent. In turn, *A. pura* and *L. coriaceum* were not collected in 2006 and 2008, while *H. modestus*, *L. zonulum*, *M. rotundata*, and *S. lateralis* were absent in 2008. Almost 60% of those species displaying an annual decline in abundante (*A. pura*, *H. confusus*, *H. modestus*, *L. coriaceum*, *L. zonulum*, *M. rotundata* and *S. lateralis*) were halictids. Conversely, only four species (75% of them from the genus *Bombus*) showed an

Table 5. Significant annual variation of genus abundance, resulting from a significant effect of year, was detected through an ANCOVA test on ranks. The effect of genus was also significant. The interaction of year-genus did not have a significant effect. Individuals were collected bi-weekly during the four years studied.

	Regression coefficient	**F-test**	**p-value**
GLM	$R^2 = 0.93$	$F_{51,52} = 12.75$	$p<<0.001$
Year		$F = 8.38$ d.f. = 1	$p = 0.006$
Genus		$F = 24.44$ d.f. = 25	$p<<0.001$
Year-Genus		$F = 1.24$ d.f. = 25	$p = 0.255$

Table 6. An ANCOVA test on ranks detected a significant annual variation of the number of bees per species, with a significant effect of year. Both the effect of species and the interaction year-species were also significant. Individuals were collected bi-weekly during the four years studied.

	Regression coefficient	**F-test**	**p-value**
GLM	$R^2 = 0.84$	$F_{113,114} = 5.48$	$p<<0.001$
Year		F = 5.07 d.f. = 1	p = 0.026
Species		F = 9.23 d.f. = 56	$p<<0.001$
Year-Species		F = 1.73 d.f. = 56	p = 0.007

Table 7. Eleven species showed a significant trend in abundance between 2003 and 2008. For these species, the number of bees collected per year from the four sites were analysed through a regression analysis. Species with decreasing abundance have been grouped apart from those species showing increases. The response variables number of bees and log (N + 0.5) were not normally distributed, hence the regression analysis was made on ranked variables; except for *Halictus confusus* whose variable number of bees was not transformed since it followed a normal distribution.

Species	Normality Test(s): Kolmogorov-Smirnov	Regression coefficient	F-test	p-value
Decrease				
Augochlora pura	D = 0.43, p<0.010 D = 0.45, p<0.010	$R^2 = 0.36$	$F_{1,14} = 7.93$	p = 0.014
Halictus confusus	D = 0.13, p>0.150	$R^2 = 0.28$	$F_{1,14} = 5.40$	p = 0.036
Hylaeus modestus	D = 0.25, p<0.010 D = 0.28, p<0.010	$R^2 = 0.38$	$F_{1,14} = 8.58$	p = 0.011
Lasioglossum coriaceum	D = 0.31, p<0.010 D = 0.38, p<0.010	$R^2 = 0.40$	$F_{1,14} = 9.46$	p = 0.008
Lasioglossum zonulum	D = 0.42, p<0.010 D = 0.28, p<0.010	$R^2 = 0.41$	$F_{1,14} = 9.68$	p = 0.008
Megachile rotundata	D = 0.34, p<0.010 D = 0.33, p<0.010	$R^2 = 0.43$	$F_{1,14} = 10.57$	p = 0.006
Stelis lateralis	D = 0.31, p<0.010 D = 0.33, p<0.010	$R^2 = 0.40$	$F_{1,14} = 9.22$	p = 0.009

Table 7. (Continued)

Species	Normality Test(s): Kolmogorov-Smirnov	Regression coefficient	F-test	p-value
Increase				
Bombus fervidus	D = 0.31, p<0.010 D = 0.33, p<0.010	$R^2 = 0.25$	$F_{1,14} = 4.65$	p = 0.049
Bombus griseocollis	D = 0.38, p<0.010 D = 0.39, p<0.010	$R^2 = 0.26$	$F_{1,14} = 4.88$	p = 0.044
Bombus impatiens	D = 0.39, p<0.010 D = 0.42, p<0.010	$R^2 = 0.28$	$F_{1,14} = 5.37$	p = 0.036
Osmia inspergens	D = 0.45, p<0.010 D = 0.48, p<0.010	$R^2 = 0.29$	$F_{1,14} = 5.72$	p = 0.031

increasing abundance (*B. fervidus*, *B. griseocollis*, *B. impatiens* and *O. inspergens*).

The proportion of bees collected among sites and disturbance levels varied annually. The difference among sites and disturbance levels progressively decreased throughout the study years until 2008 when it was lowest. The four sites (BrockNW, BrockS, Pond and St. Davids) differed annually, with an unusually high number of bees collected in 2003 due to the contribution of BrockNW and BrockS (Fig. 11; goodness of fit test: $\chi^2 = 1621.9$, d.f. = 9, $p<<0.001$). This annual pattern was also confirmed when abundance was analysed for low (BrockNW and BrockS) and high (Pond and St. Davids) disturbance levels (Table 8).

3.5. The diversity of the bee community

The number of bees varied among families, thus rejecting the null hypothesis that bee specimens were equally distributed among families (Fig. 12; goodness of fit test: $\chi^2 = 7988.4$, d.f. = 4, $p<<0.001$). The most abundant families were Halictidae and Megachilidae, followed by Apidae, Colletidae and Andrenidae. Bees were not evenly distributed among nesting guilds either (Fig. 13; goodness of fit test: $\chi^2 = 12435.8$, d.f. = 5, $p<<0.001$), with miner and mason species being much more common than other guilds. The distribution of bees among social categories (social, solitary and kleptoparasitic) was not even (Fig. 14; goodness of fit test: $\chi^2 = 3714.3$, d.f. = 2, $p<<0.001$), with solitary and social species being better represented than kleptoparasitic species. Bivoltine species predominated over univoltine and multivoltine species (Fig. 15; goodness of fit test: $\chi^2 = 4162.7$, d.f. = 2, $p<<0.001$). The species *A. mellifera* was the only representative of the multivoltine group.

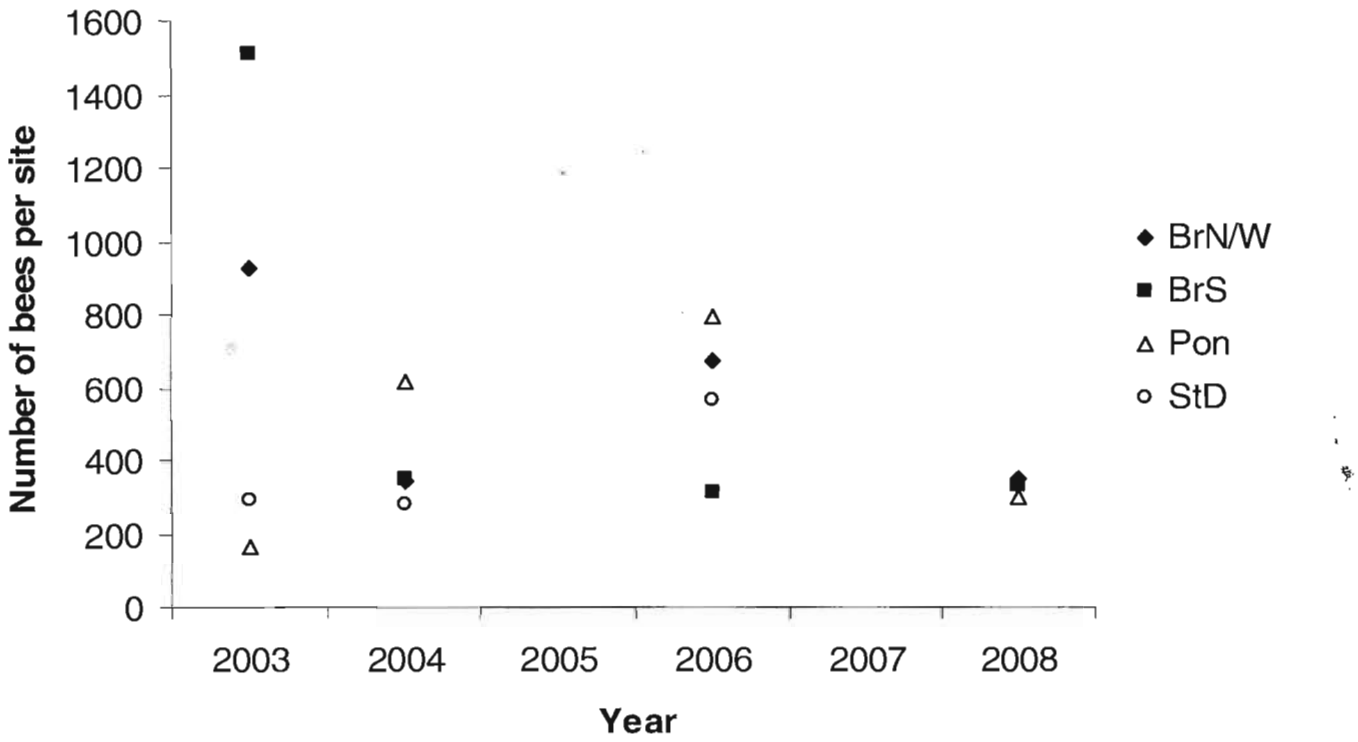


Fig. 11. Annual number of bees per site. The number of bees was the highest in BrockS and BrockNW in 2003; however it declined in subsequent years.

Table 8. The number of bees per disturbance level (low and high), where *n* denotes the number of sites.

	Low (n=2)	High (n=2)	Total
2003	2434	454	2888
2004	698	901	1599
2006	980	1358	2338
2008	680	634	1314
Total	4792	3347	8139
Goodness of fit test	$\chi^2 = 1228.1$, d.f. = 3, $p<<0.001$		

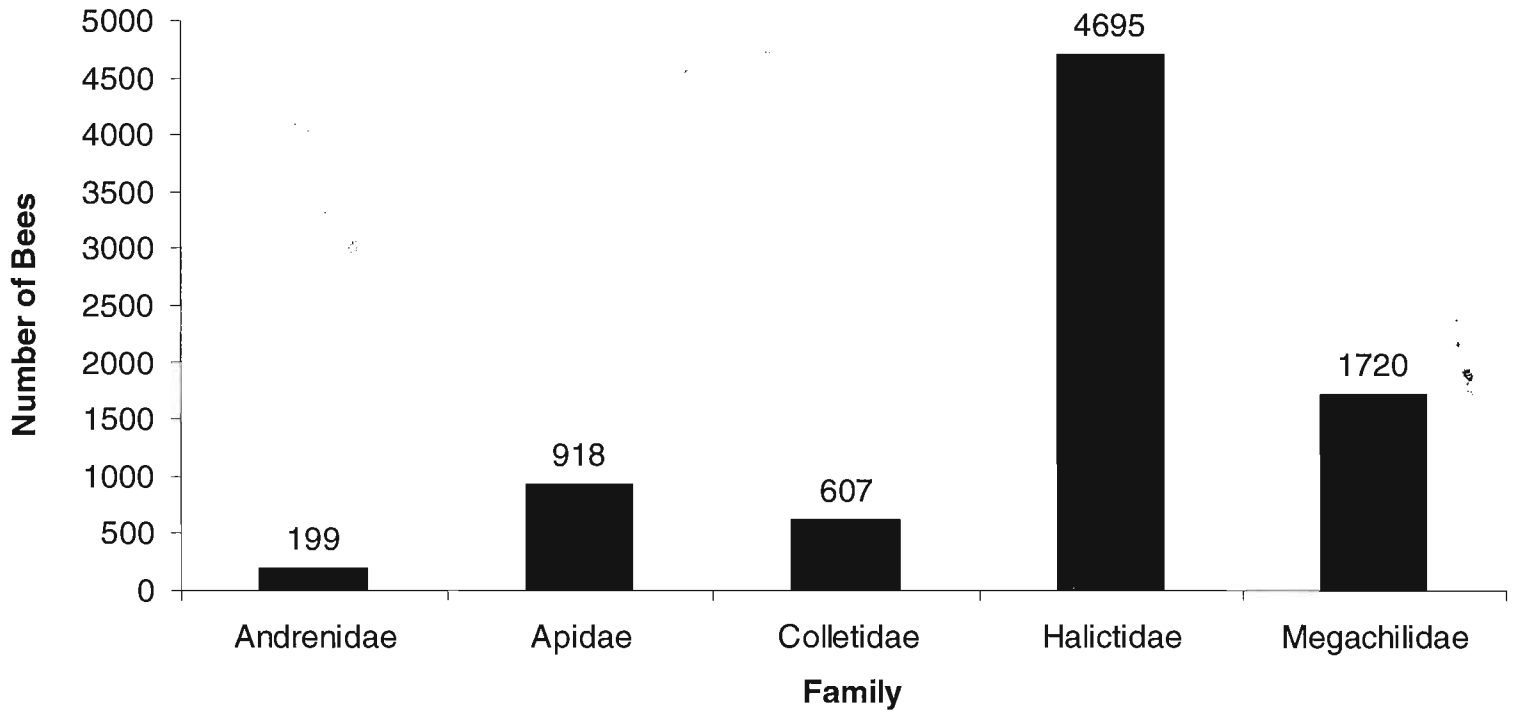


Fig. 12. The distribution of number of bees among families. The dataset of four pooled years was obtained from a bi-weekly series.

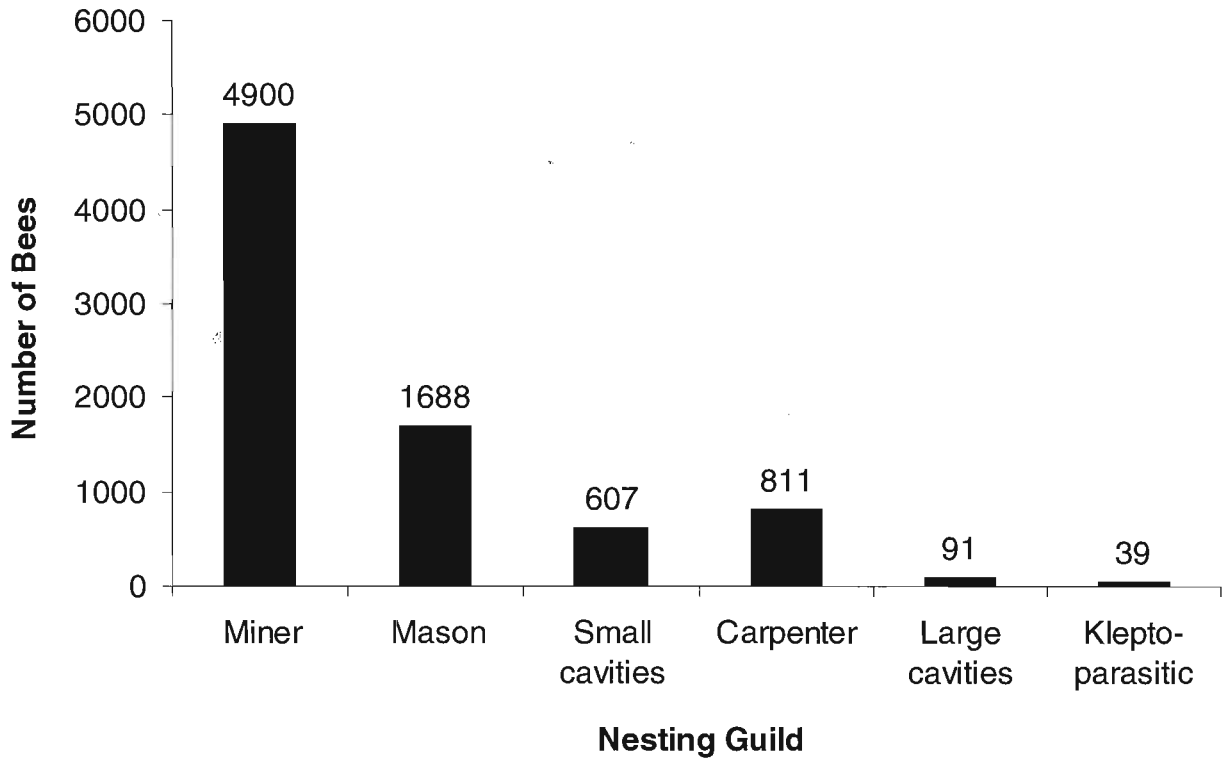


Fig. 13. Distribution of the number of bees per nesting guild. Miner and mason species were the most abundant nesting guilds. The collected data of four years were pooled in a bi-weekly frequency from the sites BrockNW, BrockS, Pond and St. Davids.

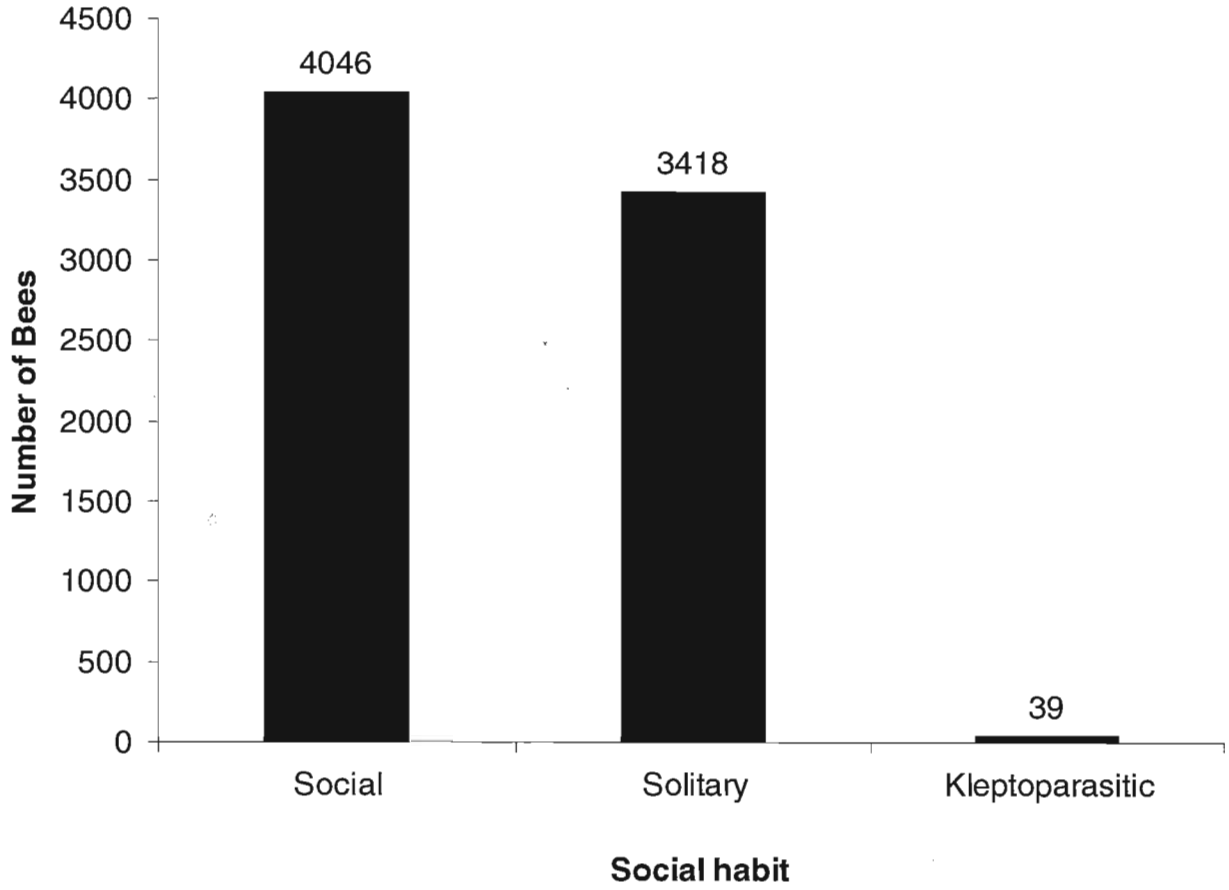


Fig. 14. Distribution of the number of bees per social habit. Social species were more abundant than solitary and kleptoparasitic species. The collected data of four years have been pooled in a bi-weekly frequency from the sites BrockNW, BrockS, Pond and St. Davids.

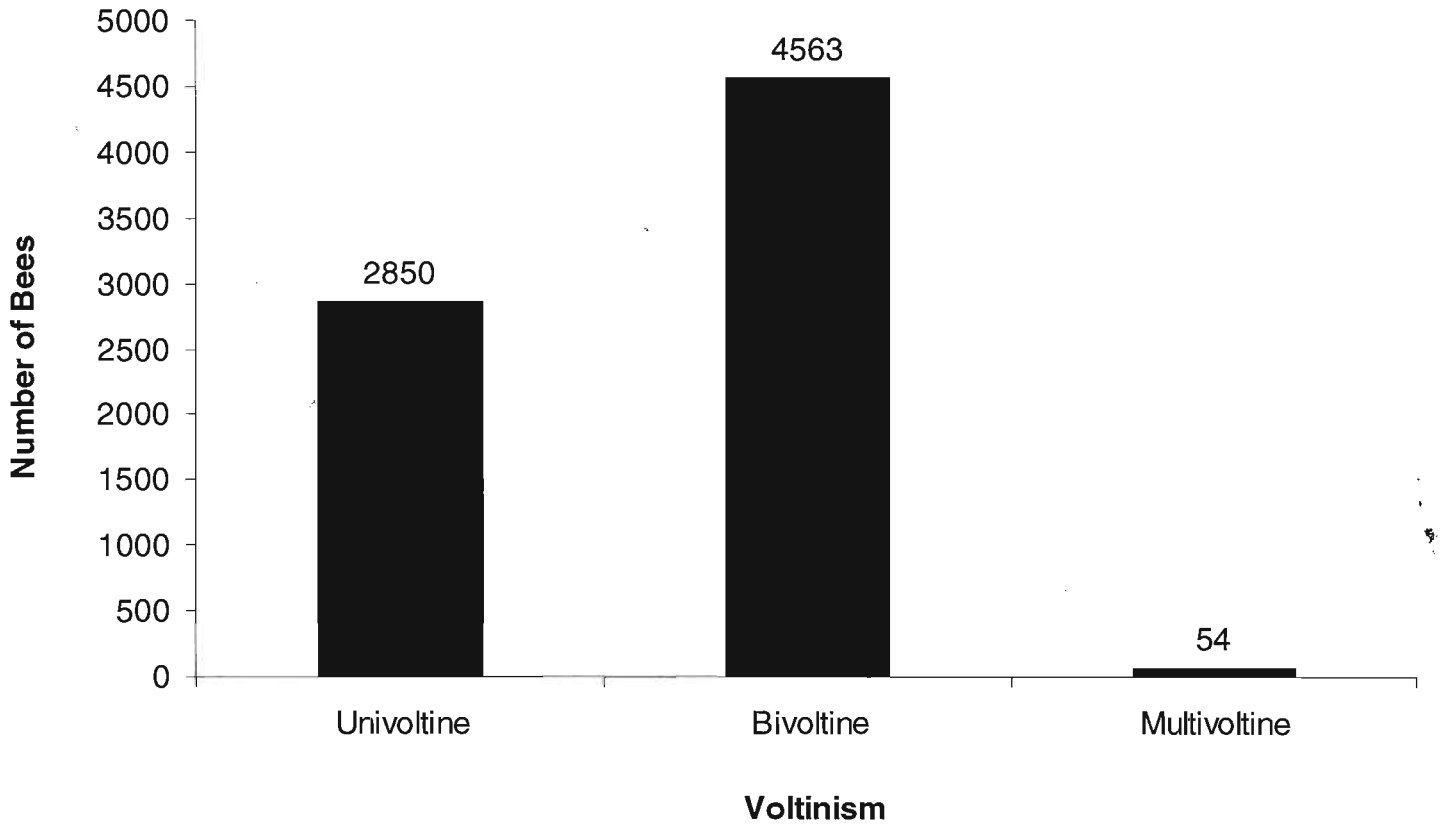


Fig. 15. Distribution of the number of univoltine, bivoltine and multivoltine species. The collected data were pooled in a bi-weekly frequency from the sites BrockNW, BrockS, Pond and St. Davids.

3.6. Annual variation in diversity

The total diversity of the bee community varied annually; in addition the total bee diversity present at the sites was presumably not collected each year. Therefore, to estimate the total number of genera and species that was likely present, the ACE and Chao-1 estimators were calculated for the overall four years studied and for each year. The estimation of the generic richness present in the four years studied suggested a total of 27 genera, whereas the number of observed genera was 26 (Table 9). For each year the 95% confidence intervals included the total generic richness observed over the four years studied. The highest estimate for the total number of genera was suggested for 2003 with 30 genera (Chao-1 95% C.I. = 24.9 – 62.7), while the observed generic richness that year was 24. The estimated total number of genera for 2004 was 25 (Chao-1 95% C.I. = 19.9 – 57.5), while the observed genera were 19. In both years, a greater generic richness could have been caught, as suggested by the difference between the estimated and observed genera, and the high upper values for confidence intervals. Conversely according to the ACE and Chao-1 estimates, in 2006 and 2008 almost all the genera that were present were collected. The 2006 and 2008 estimates (22 and 17 genera, respectively) were close to the observed number of genera (21 and 16 genera, respectively), with both years having narrower confidence intervals than 2003 and 2004. These annual differences were also reflected in the rarefaction curves of genera that were calculated for each year and the overall four years studied (Fig. 16). The year 2008 yielded the least diversity (16 genera) with the lowest sample size (1314 bees) and number of genera per individual. For the four years studied, the number of genera was about 20 when 1314 bees had been collected. The year 2003 yielded the most generic richness per number of individuals

Table 9. Estimation of the total generic richness for the four years studied, using the Abundance-based Coverage Estimator (ACE) and the Chao-1 estimator. Both estimations were performed using EstimateS with 50 randomisations on each dataset. The 2006 total number of genera was estimated using the classical Chao-1; the bias-corrected version was used in 2003, 2004 and 2008 when there were no doubletons.

Data subset	Number of Genera	ACE	Chao-1 (mean ± SD)	Chao-1 95% C.I.
All-years	26	27.4	27.0 ± 1.9	26.1 – 37.1
2003	24	30.0	30.0 ± 7.3	24.9 – 62.7
2004	19	25.0	25.0 ± 7.2	19.9 – 57.5
2006	21	21.3	21.7 ± 1.3	21.1 – 28.8
2008	16	17.0	17.0 ± 2.3	16.1 – 30.2

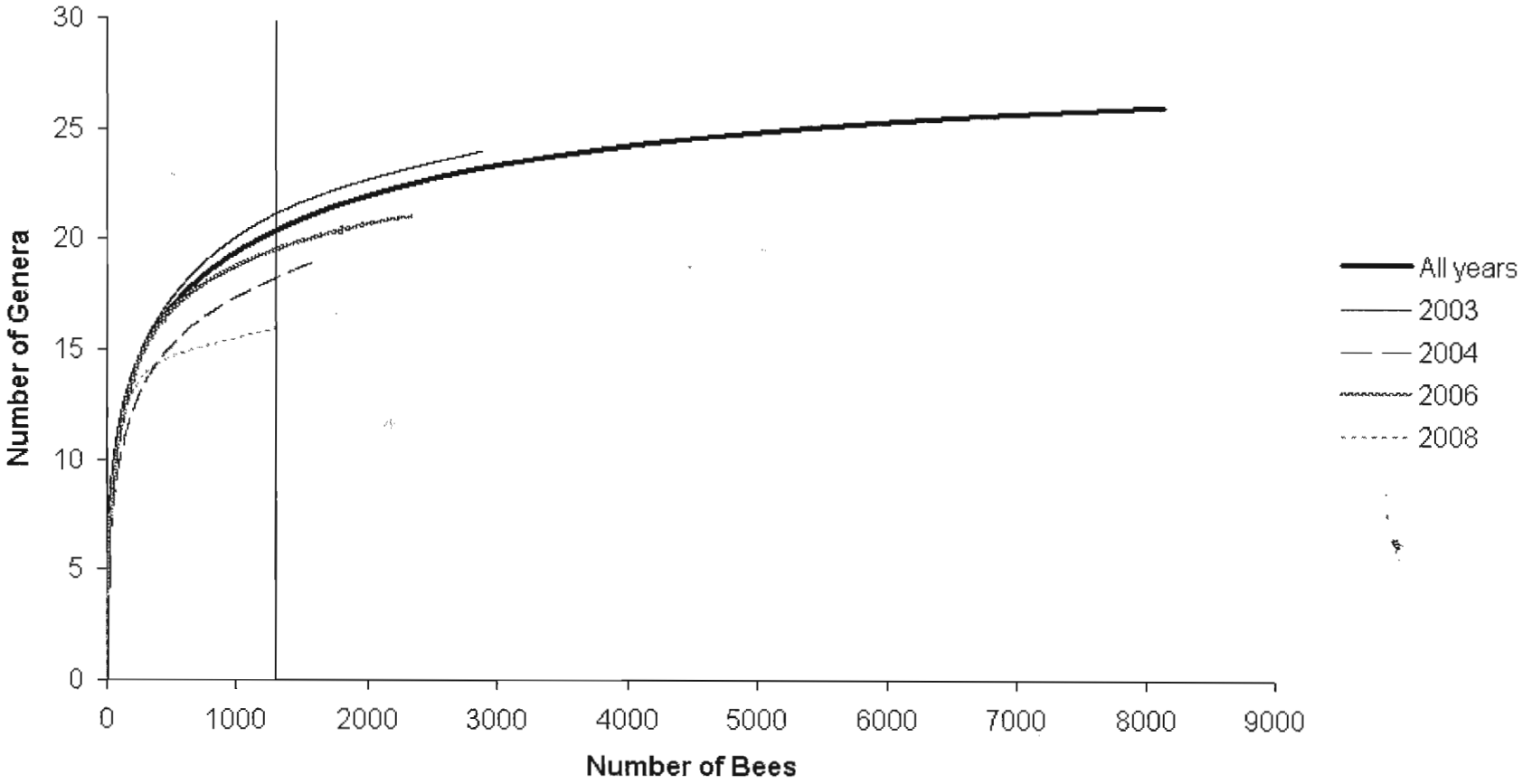


Fig. 16. Rarefaction curves for the four years studied comparing the number of genera collected bi-weekly at four sites. The vertical line represents the sample size (1314 bees) of the year 2008, which is used to compare the generic richness variation among years.

collected (about 21 genera at the cut-off of 1314 bees), contributing the most to the total number of genera identified over the four years studied. The steep curve of 2004, with 18 genera when 1314 bees were captured, indicates that a greater number of genera could have still been collected. Conversely, the second richest year was 2006 with about 20 genera at the cut-off of 1314 bees, having a flatter slope than 2004 due to the lower rate at which new genera per individual were added.

The species richness estimation for the four years studied suggested by the ACE estimator totalled about 62 species while the observed species richness was 57 (Table 10). For each year, the observed species richness was lower, although the respective confidence intervals included the observed species richness of the four years studied. The highest estimate was suggested for 2003 totalling about 70 species (Chao-1 95% C.I. = 48.7 – 155.5) while the observed species richness that year was 42. In 2003 the number of species collected could have been still higher, due to the existing difference between the estimated and observed species richness, and the high upper value of the confidence interval. In 2004, the estimated total number of species was 42, while the observed species richness was 34 species. On the other hand, in 2006 the observed 45 species was the highest species richness among years, whereas the estimated total number of species was about 50 (Chao-1 95% C.I. = 46.0 – 64.9). This suggests that in 2006 almost all the species that were present were collected. Similarly, almost all the species present in 2008 were collected, with an estimated total of 33 species (Chao-1 95% C.I. = 28.8 – 60.1) and 28 species observed. These annual changes were also identified in the rarefaction curves that were calculated for the four year studied and for each year (Fig. 17). The year 2008 yielded the lowest species richness per individual, with the lowest number of individuals

Table 10. Estimation of the species richness for the four years studied, using the Abundance-based Coverage Estimator (ACE) and the Chao-1 estimator. Both estimations were performed using EstimateS with 50 randomisations on each dataset. Estimates for 2004 and 2006 were calculated using the classical Chao-1; the bias-corrected version was used in 2003 and 2008 when there was just one doubleton. Collections were made bi-weekly at four sites; *Andrena*, *L. (Dialictus)* and *Nomada* were not included in the calculations.

Data subset	Number of Species	ACE	Chao-1 (mean ± SD)	Chao-1 95% C.I.
All-years	57	61.5	60.1 ± 3.1	57.6 – 72.9
2003	42	69.5	69.5 ± 22.8	48.7 – 155.5
2004	34	39.6	42.0 ± 7.5	35.7 – 71.8
2006	45	48.6	49.5 ± 4.0	46.0 – 64.9
2008	28	33.0	33.0 ± 6.1	28.8 – 60.1

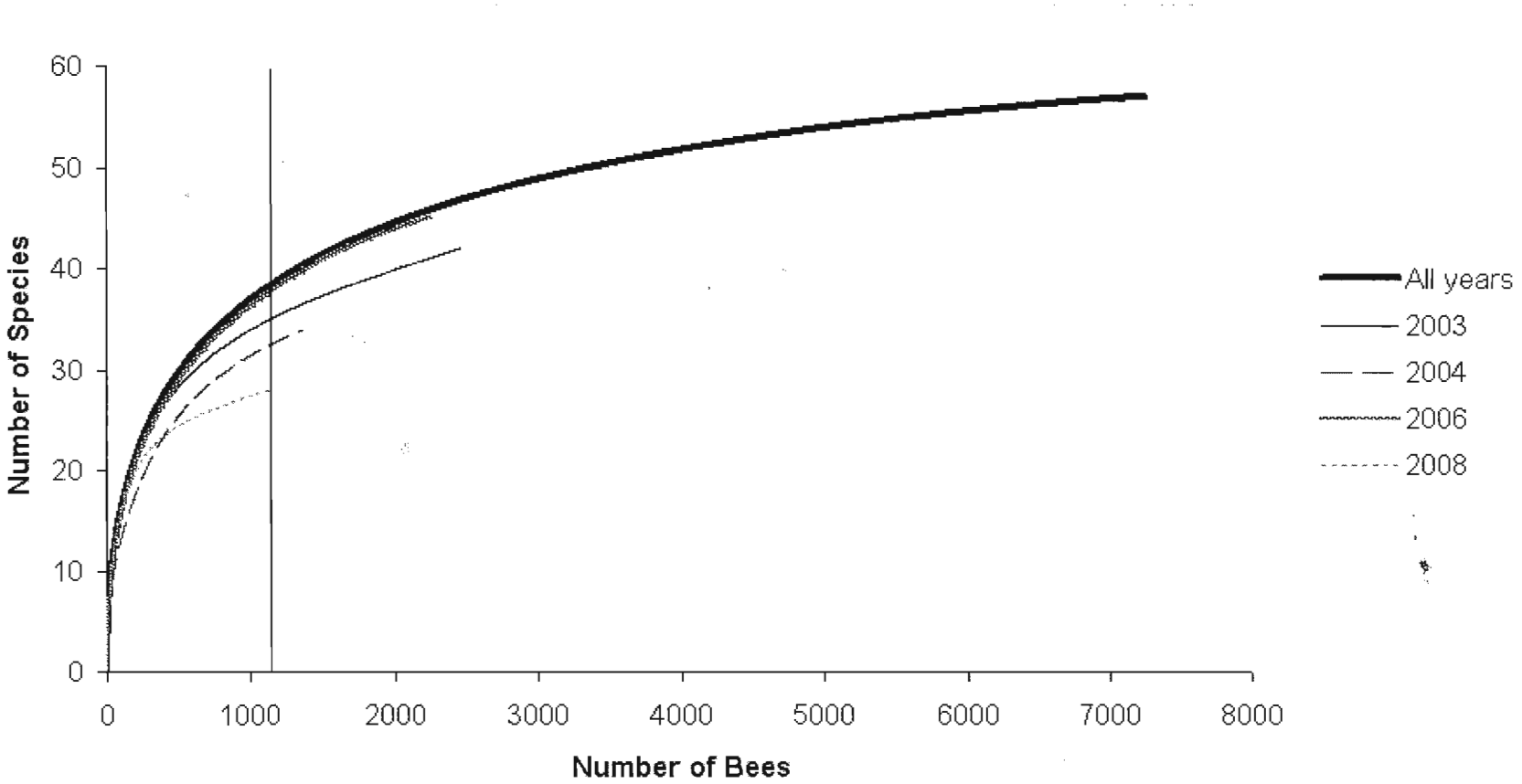


Fig. 17. Species rarefaction curves comparing the number of species collected bi-weekly at four sites over the four years studied. The vertical line represents the cut-off of 1139 bees collected in 2008, with which the species richness comparison among years is made.

and species collected (1139 bees and 28 species). For the four year studied, about 38 species were collected at the cut-off of 1139 bees. The year 2006, with 1139 bees and about 38 species, yielded the highest species richness per number of individuals collected, contributing the most to the species richness of the four year studied. In 2003, when most of the bees were captured, 1139 bees yielded 35 species. The slope of the curve for 2004 at the cut-off of 1139 bees (with 32 genera) suggests that a greater number of species could have been collected that year.

When the effect of abundance was controlled, the generic and species richness also varied among years, with species richness being comparatively more variable. The numbers of genera collected in 2003, 2004 and 2006 were not significantly different than expected, while in 2008 the number of genera collected was significantly lower than expected (Table 11). The numbers of species collected in 2003, 2004 and 2008 were significantly lower than expected, while the number of species collected in 2006 was not significantly different than expected (Table 12).

The annual variation pattern of genus and species composition supported the hypothesis that turnover of genera and species would increase over time. The Abundance-based Jaccard Index used pairs of years to estimate the similarity of genus and species composition over the four years studied (Table 13). Similarity in genus composition was over 99% (with 99.9% in 2004-2006) for periods of 1 to 3 years, decreasing similarity for longer intervals of time because fewer genera were shared. Species composition similarity was over 99% for periods of time of less than 2 years (with 98.2% in 2006-2008), and progressively decreasing to just 92% for the five-year period. This decreasing similarity pattern was a reflection of the increasing annual

Table 11. The mean expected number of genera was estimated through a randomisation analysis which generated a frequency distribution of the expected number of genera (Richardson and Richards, 2008). In addition, the standard deviation, and the 95% Confidence Interval (C.I.) of this generated frequency distribution were also calculated. The randomisation analysis was performed in order to test the null hypothesis that the number of genera did not vary among years. The observed number of genera was compared to the 95% C.I. of the expected frequency distribution in order to identify significant differences among years. When the observed number of genera values fell within the 95% C.I., there were not significant differences among the observed and mean expected values. Alternatively, significant differences between the observed and the mean expected number of genera existed when the observed values (in bold) fell outside the 95% C.I.

	2003	**2004**	**2006**	**2008**
Observed Number Genera	24	19	21	**16**
Mean Expected Number Genera	23.22	21.15	22.52	20.44
Standard Deviation	1.22	1.44	1.31	1.49
95% Confidence Interval range	20.83-25.60	18.33-23.96	19.95-25.09	17.51-23.37

Table 12. The mean expected species richness was estimated through a randomisation analysis which generated a frequency distribution of the expected species richness (Richardson and Richards, 2008). In addition, the standard deviation, and the 95% Confidence Interval (C.I.) of this generated frequency distribution were also calculated. The randomisation analysis was performed in order to test the null hypothesis that the species richness did not differ among years. The observed species richness was compared to the 95% C.I. of the expected frequency distribution in order to identify significant differences among years. When the observed species richness values fell within the 95% C.I., there were not significant differences among the observed and mean expected values. Alternatively, significant differences between the observed and the mean expected species richness existed when the observed values (in bold) fell outside the 95% C.I.

	2003	2004	2006	2008
Observed Species Richness	**42**	**34**	45	**28**
Mean Expected Species Richness	46.80	40.47	45.85	38.38
Standard Deviation	2.27	2.53	2.31	2.58
95% Confidence Interval range	42.35-51.24	35.51-45.44	41.33-50.37	33.32-43.44

Table 13. The genus and species (taxa) composition similarity was analysed in order to test the hypothesis that the taxa turnover would increase with years. The computer program EstimateS was used to analyse the similarity change among pairs of study years (Colwell, 2009). The Abundance-based Jaccard (J_{abd}) Index was adjusted for the *unseen* taxa of the bee community (Chao *et al.*, 2005). Values close to 1 represented a high similarity while values close to 0 would represent a total dissimilarity. This index accounted for the sample size variation among years and also considered the rare shared taxa that might not be detected (*unseen*) in the smaller samples. For each year pair, the number of shared genera and species was also shown.

Year(s) lapsed	Years	Number Shared Genera	J_{abd} for genera	Number Shared Species	J_{abd} for species
1	2003-2004	17	0.996	27	0.992
2	2004-2006	18	0.999	30	0.990
2	2006-2008	15	0.990	25	0.982
3	2003-2006	19	0.993	32	0.986
4	2004-2008	13	0.985	21	0.961
5	2003-2008	16	0.988	22	0.923

turnover of genera and species experienced by the bee community. This trend was more consistent for species than for genera and for periods of four and five years than for periods of three years or less.

The proportions of bees collected according to family varied annually (Fig. 18; goodness of fit test: $\chi^2 = 872.7$, d.f. = 12, $p<<0.001$). The family Halictidae represented the most abundant family over the four years studied ranging from 57% to 76% of the bees collected for the first three study years. However, this family decreased to just 38% of specimens in 2008, when Halictidae were nearly equal in abundance to Megachilidae. The family ranks did not vary among years, except for 2006 when bees in the family Colletidae were exceptionally common relative to other years. According to nesting guild, the proportion of bees in each guild differed annually (Fig. 19; goodness of fit test: $\chi^2 = 837.4$, d.f. = 15, $p<<0.001$). Miner and mason bees were the most abundant guilds for the four years studied, although in 2008 miner bees decreased to just 42% while in previous years they represented between 60% - 80% of bees collected. However, except for 2006 when small cavity nesters (with 15% of the total bees collected) were more abundant than carpenter bees (4%), ranks for the remaining guilds remained relatively stable over the four years studied. Annual variation was also detected in the proportion of bees per social habit (Fig. 20; goodness of fit test: $\chi^2 = 405.8.7$, d.f. = 6, $p<<0.001$). Social bees were most abundant in 2003, 2004 and 2006 ranging from 50% to 73% of the bees collected. The proportion of social bees decreased to just 35% in 2008 when solitary bees became more abundant. Solitary bees were almost as abundant as social bees in 2003, but decreased by almost three-fold the following year. Kleptoparasitic bees were consistently low over the four years studied. In terms of voltinism, the proportion of bees

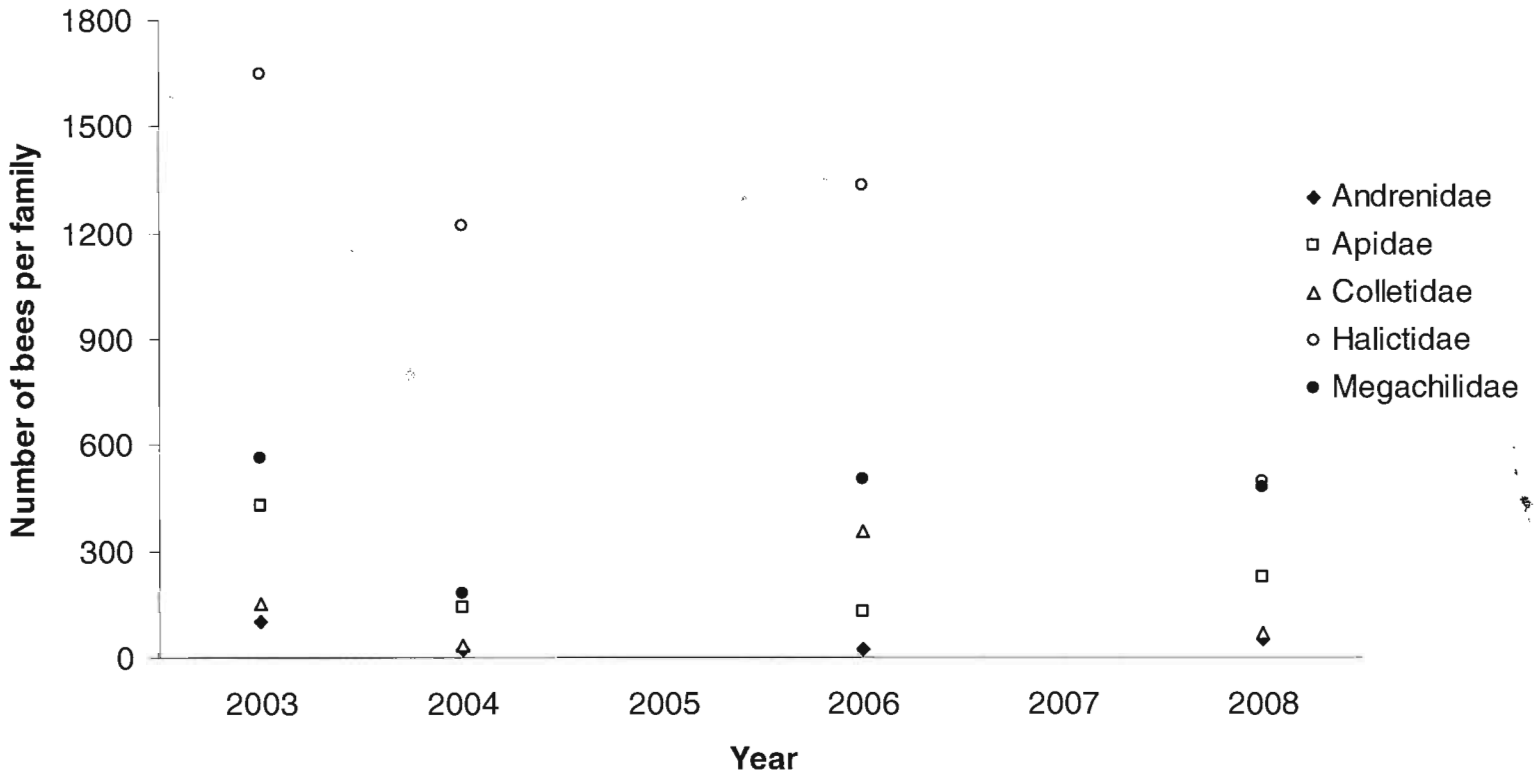


Fig. 18. Annual variation of the number of bees per family. In relation to previous years, in 2008 the family Halictidae decreased abruptly.

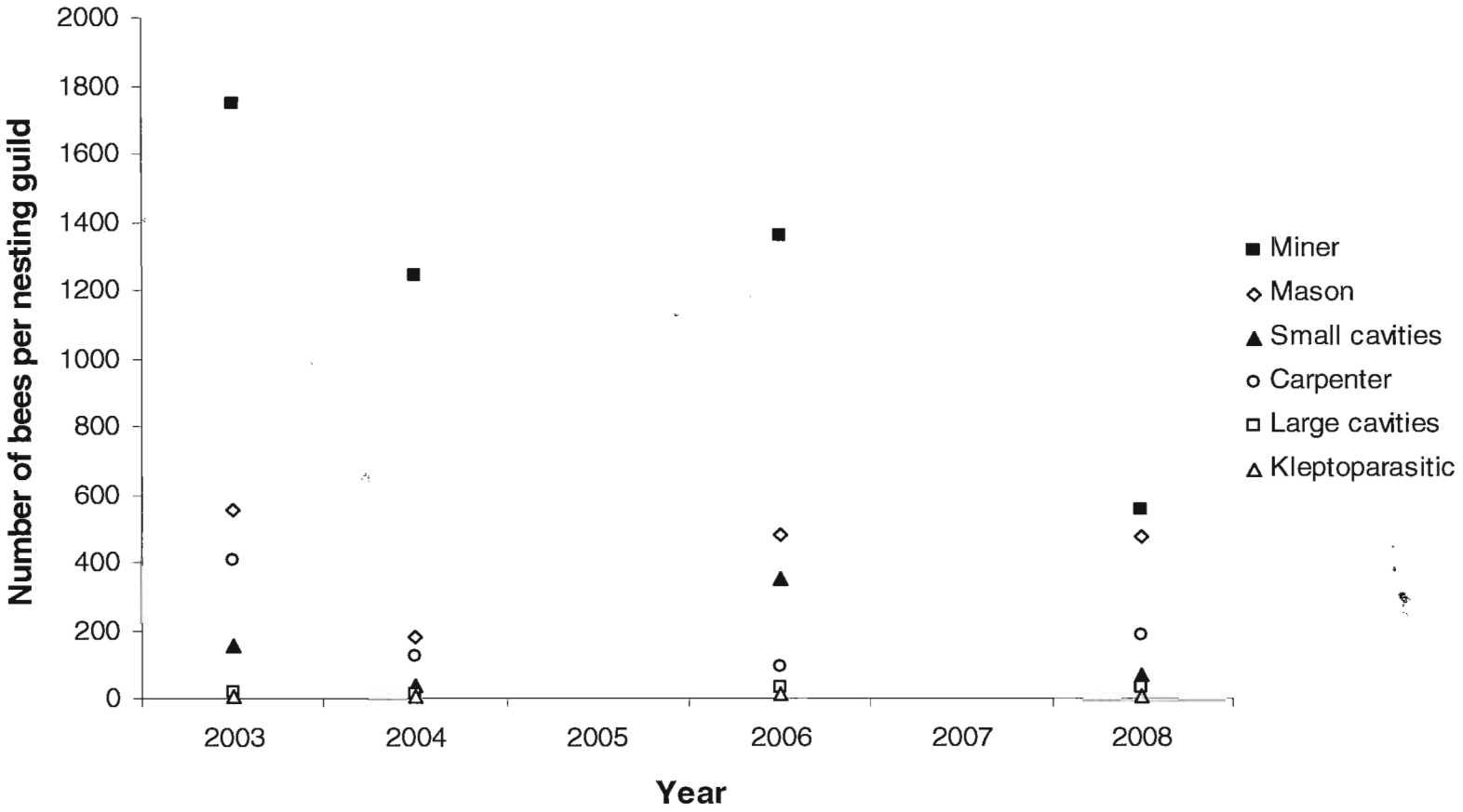


Fig. 19. Annual variation of the number bees in each nesting guild. The miner species, the most abundant guild over the first study years, decreased in 2008 by two-fold. Conversely, the other guilds did not vary that much over the four years studied.

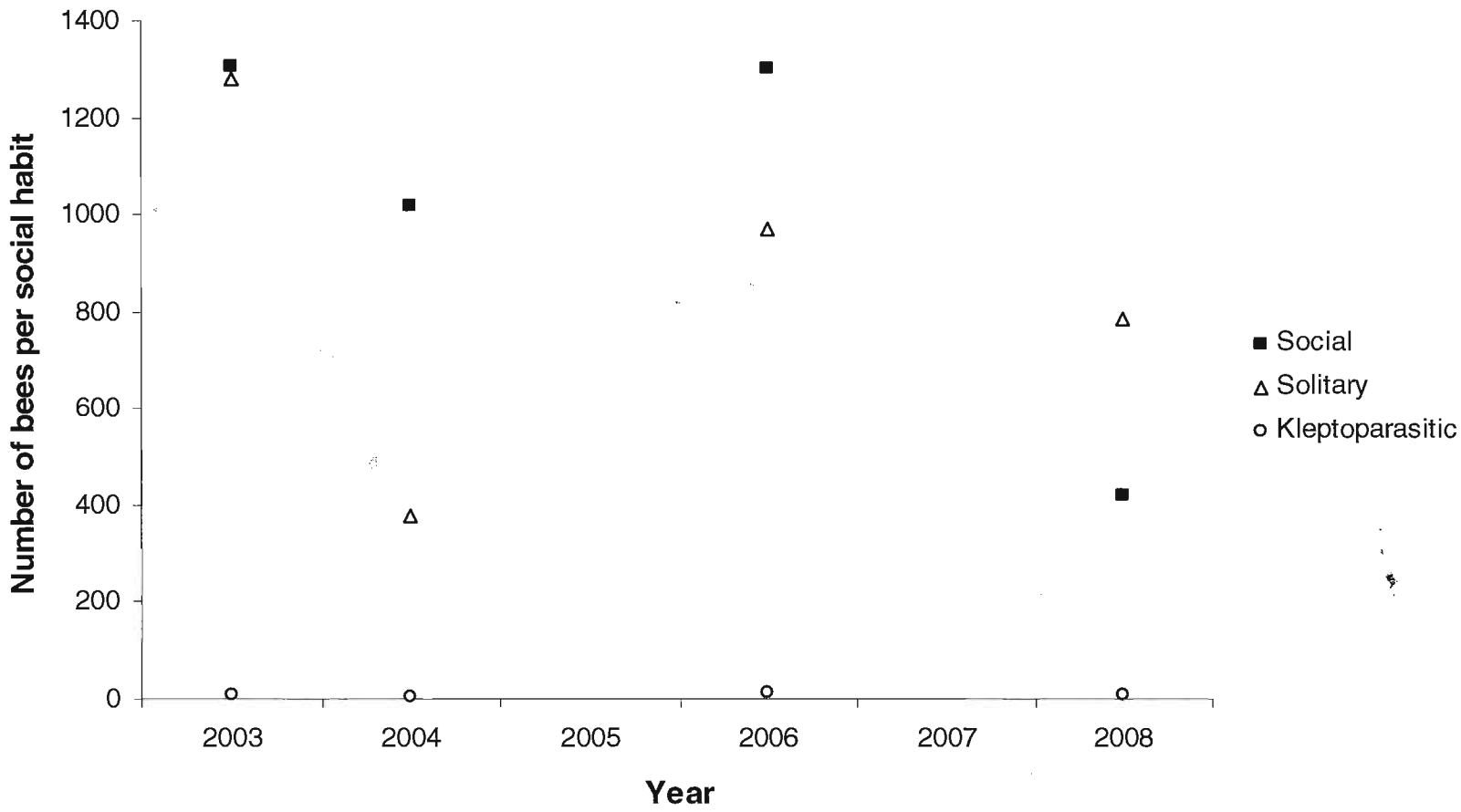


Fig. 20. Annual distribution of the number of bees according to their social habit. The social species predominated in 2003, 2004 and 2006, although the solitary species predominated in 2008.

collected also varied from year-to-year (Fig. 21; goodness of fit test: $\chi^2 = 513.2$, d.f. = 6, $p<<0.001$). Bivoltine bees were the most abundant for the first three study years, decreasing over two-fold in 2008 when univoltine bees became more abundant. From 2003 to 2004 univoltine bees decreased from 44% to 25% of the bees collected although they gradually increased by the end of the study period. Multivoltine bees consistently represented a low number of bees over the four years studied.

The annual pattern of variation for the proportion of bees according to family, nesting guild, social habit and voltinism was due to the annual variation of the most abundant taxa. These taxa included *A. aurata*, *H. confusus*, *H. ligatus*, *L. (Dialictus)*, *C. dupla/mikmaqi*, *C. calcarata*, *H. affinis*, and *O. conjuncta*. The halictid taxa combined (*A. aurata*, *L. (Dialictus)*, *H. confusus* and *H. ligatus*) were more abundant than the rest of the abundant taxa in 2003 with 1550 bees, 2004 with 1188 bees and 2006 with 1279 bees. In 2008, *C. dupla/mikmaqi*, *C. calcarata*, *H. affinis* and *O. conjuncta* with 576 bees were more abundant than the halictid taxa that decreased to 472 bees. Nevertheless, the abundant (and especially the halictid) taxa exerted the most important influence on the annual variation pattern exhibited by the whole bee community. The influence of the halictid taxa was reinforced by the fact that, in addition to sharing family and nesting guild, they were also social and bivoltine species except for *L. (Dialictus)*. Conversely, the variety of families and nesting guilds displayed by *C. dupla/mikmaqi*, *C. calcarata*, *O. conjuncta* and *H. affinis* lessened their influence on the annual variation of the bee community.

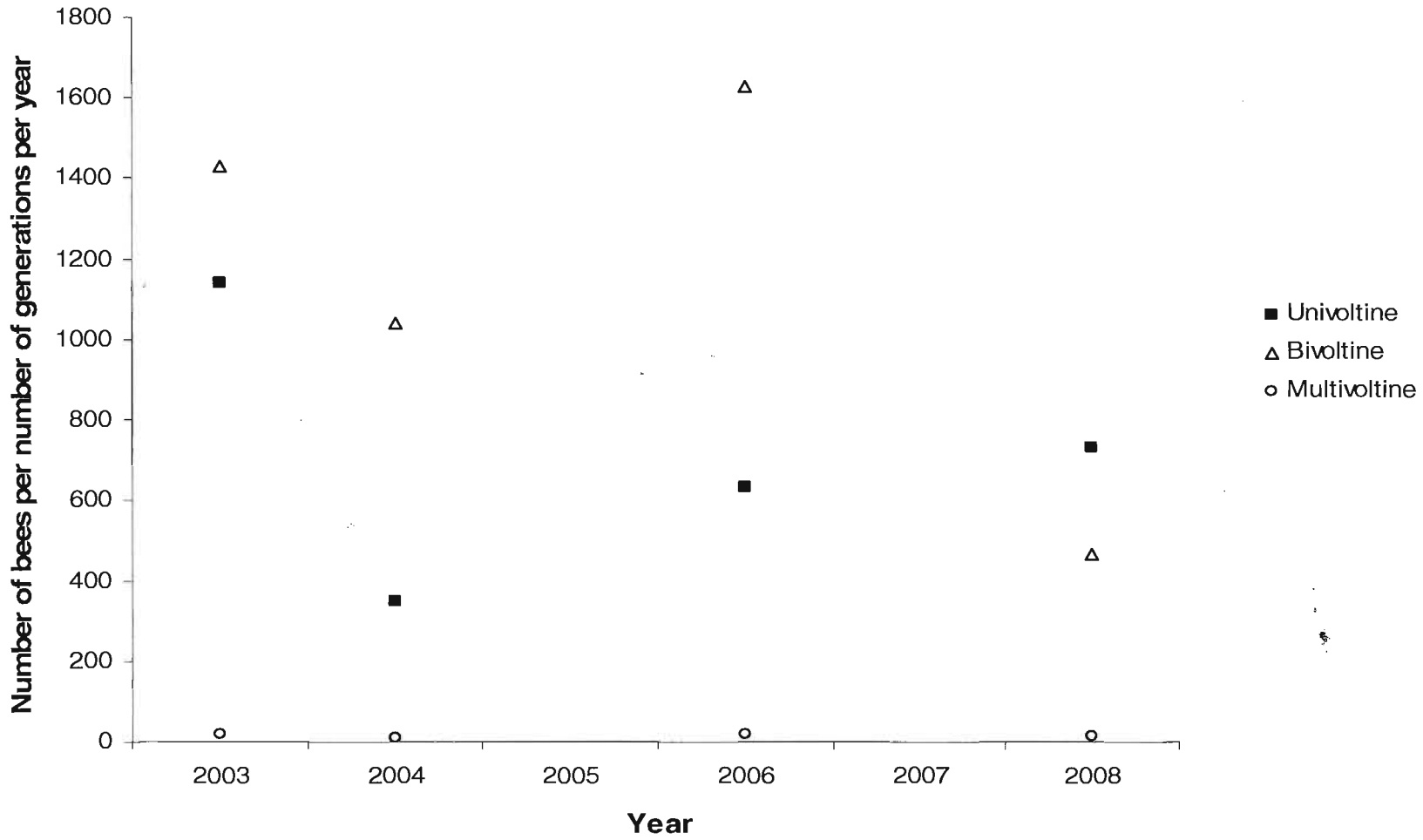


Fig. 21. Distribution of the number of bees according to the number of generations per year. Bivoltine species decreased importantly in 2008.

4. DISCUSSION

This study strongly supports previous reports that bee communities exhibit annual variation in abundance and diversity. There was significant variation among 2003, 2004, 2006, and 2008. This study was the first to assess the annual variation of abundance and diversity in a bee community of the Niagara Region; it also comprised a bee collection of four years, constituting the longest bee survey performed in Canada to date.

4.1. General aspects of the bee community

This bee community was found to be relatively diverse with the presence of 26 genera and sub-genera and at least 57 species (excluding *Andrena, L. (Dialictus)* and *Nomada*) belonging to the 5 families found in eastern North America. The actual species richness of the Niagara Region should be greater, when more locations are sampled and full identification of the above taxa to species level is completed. Nevertheless, the detection of newly introduced species and the collection of transient and rare species has also increased in relation to the 2003 survey, after the sampling effort was extended over the period covered by this study. Indeed, for 2004, 2006 and 2008 the complete species list of the bee community included recently introduced species and rare species not collected in 2003 (please refer to Appendix II). The invasive species *Anthidium oblongatum* that has been recently expanding its distribution in North America (Maier, 2009; Miller *et al.*, 2002) was recorded in Niagara in 2006 and 2008. Other rare and transient species collected in 2004, 2006 and 2008 included *B. griseocollis*, *B. mixtus*, *B. perplexus*, *B. sandersoni*, *B. vagans*, *C. banski*, *C. rufitarsis*, *H. illinoisensis*, *H. truncata,*

L. (E.) macoupinense, *M. apicata*, *M. campanulae*, *M. centuncularis*, *M. inermis*, *M. montivaga*, *M. relativa*, *O. inspergens*, *S. heraclei*, and *T. simplex*.

4.2. Phenology of the bee community

This study confirmed previously detected seasonal variation patterns of this bee community of the Niagara Region (Richards *et al.,* 2011; Rutgers-Kelly, 2005). Moreover, the results supported the hypothesis that the number of bees collected in spring would be significantly higher than those collected in summer.

This bee community was characterized by three distinct periods of flight activity over the four years studied (early spring, late spring/early summer, and late summer). This pattern was also detected in previous surveys of Niagara and other locations (Oertli *et al.,* 2005; Richards *et al.,* 2011; Rutgers-Kelly, 2005). Bees that overwinter as adults, belonging to the genera *Osmia*, *Ceratina* and *Andrena*, appeared in early spring (Weeks 1-5). The abundance of these bees for the four pooled years did not reach a peak in Week 1, differing from the study of Richards *et al.* (2011). For these genera, peaks in Week 1 were only recorded in 2003 and 2006; in 2004 and 2008 their highest peak occurred in Week 5, which represented a delay. In Week 5, the first peak for the four years studied occurred and it result from a high foraging activity of *A. aurata* foundresses, in addition to the high activity of the above taxa detected in 2004 and 2008.

The summer solstice (Week 11) coincided with declining flight activity for all years except for 2006 (when the decline occurred in Week 7). This low activity is mostly due to a quiescent period between the provisioning and emergence of the worker brood of bivoltine and eusocial species. The second peak detected occurred in Week 13 in all years

except for 2006 (when it occurred in Week 11). This corresponded to the activity of the worker brood of bivoltine and eusocial species, in addition to the emergence of adults in the genera *Hylaeus* and *Megachile*, which had overwintered as juveniles and developed further in spring (Richards *et al.*, 2011). Furthermore, in late summer a third seasonal peak occurred in Week 19, with high flight activity of the reproductive brood of bivoltine and eusocial species.

Generally, the flight activity in 2003 and 2006 was greater than in 2004 and 2008. This supported the hypothesis that the seasonal flight activity for both the overall community and the abundant species would vary among years. There was also a high annual variability in the length of seasons and the occurrence of flight activity peaks, with the seasons of 2003 and 2006 being longer and more advanced than in 2004 and 2008. These annual changes in bee phenology might be due to inter-annual differences in temperature and annual precipitation; that affect the growing season length and the availability of flower and nesting resources (Gordo and Sanz, 2006; Richards and Packer, 1995, 1996; Richards, 2004; Roulston *et al.*, 2011; Tuell and Isaacs, 2010). Weather influences the behaviour and life cycle of bees, which find their optimal conditions during moderately dry and warm weather; and this has an effect on their activity as pollinators (Gordo and Sanz, 2006; Karise *et al.*, 2010; Lyon; 1992; Pitts-Singer and James, 2010; Tuell and Isaacs, 2010). Warm years may favour longer bee seasons, in which several life cycles are completed within a season, resulting in an overall increase in the number of bees of the community (Gordo and Sanz, 2006; MacKay and Knerer, 1979; Richards, 2004; Richards and Packer, 1995; Weissel *et al.*, 2006). Conversely, colder temperatures and rainfall fluctuations between years may be related to slower

development, diseases, nest failure and lower foraging activity, and, in extreme cases, may cause mortality, smaller brood and colony sizes and lower numbers of bees (Lyon; 1992; Pitts-Singer and James, 2010; Richards and Packer, 1995, 1996; Richards, 2004; Tuell and Isaacs, 2010).

Bivoltine species such as *A. aurata* and *H. ligatus* responded differently than the univoltine species *C. dupla/mikmaqi* and *C. calcarata* to this annual variability. In 2006, the two bivoltine species occurred earlier than other years (in Week 1), while *C. dupla/mikmaqi* and *C. calcarata* occurred later than other years (in Week 5). Inter-annual delays in the early flight activity of univoltine and bivoltine (first brood) species may be the result of fluctuations in flower resource availability in the previous year (Gordo and Sanz, 2006; Herrera, 1988; Roulston and Goodell, 2011).

4.3. Abundance of the bee community

The study of Richards *et al.* (2011) was used as a reference to assign each genus to a specific abundance category (abundant, common or rare). The bee community was characterized by considerable consistency of abundance categories between years, in proportional representation and composition of genera. However, the stability in genus composition decreased with abundance. The abundant genera did not differ between the two studies; 19 common and rare genera were shared (although *Melissodes* was rare in this study). Three rare genera (*Chelostoma*, *Colletes* and *Heriades*) present in the study of Richards *et al.* (2011) were not collected in this study, while the opposite was true for *Triepeolus*. A similar stability pattern was also observed for species abundance categories, with both studies sharing the same abundant species. However, the abundance

of common and rare species was variable than was the abundance of genera, with 35 species remaining at the same categories, while 21 species changed status between common and rare species or were not collected in one of the studies.

Regarding disturbance, this study partially supported (since intermediate disturbance levels were not studied) the Intermediate Disturbance Hypothesis tested on this bee community by Rutgers-Kelly (2005). As expected, the proportion of bees over the four years pooled was higher in the Brock sites subject to low disturbance levels, than in Pond and St. Davids where disturbance level was regarded as high. This would be the result of the differences of nesting resources, plant cover and plant abundance among sites experiencing different degrees of disturbance (Grundel *et al.,* 2010; Quintero *et al.,* 2010; Roulston and Goodell, 2011). This is a very common pattern in urban, suburban and agricultural landscapes, which have habitat patches of mixed disturbance levels (Roulston *et al.,* 2011; Winfree *et al.,* 2007).

4.4. Annual variation in abundance

Over the four years studied, there was annual variation in genus and species abundance, with the abundant genera and species differing from the less common and rare taxa. This supported the hypothesis that the more abundant genera (or species) would occur more consistently over the years and would not move to other abundance categories as often as their less common and rare counterparts. Twelve abundant and common genera consistently occurred over the four years studied and remained in the same abundance category, not including *Hylaeus* in 2004 and *L. (Dialictus)* in 2006, which changed from abundant to common genera. Conversely, the remaining genera

varied from common to rare over the four years studied and were not present at all in at least one year (except for *Bombus*). Thirteen abundant and common species were consistently collected over the four years studied, remaining in the same abundance category. The exceptions were *H. affinis* in 2004, and *C. calcarata* and *C. dupla/mikmaqi* in 2006 that changed from abundant to common species. The remaining common and rare species were more variable and were not collected in at least one study year (except for *H. producta*, *Megachile brevis* and *M. latimanus*).

This study also supported the hypothesis that the number of bees collected according to genus and species would differ among years. The bee community was subjected to annual abundance fluctuations as reflected by annual variation of the number of bees collected per genus and per species, with a declining trend over the four years studied that was detected by the ANCOVA tests. These tests identified a significant linear relationship between the number of bees collected per genus and species and year, although the relationship was stronger for genera than for species. Consequently, the annual effect was highly significant for genera, while it was significant for species. This might be explained by the fact that the ANCOVA test for genera included all the available individuals, while *Andrena*, *L. (Dialictus)* and *Nomada* were excluded from the analysis of species. Nonetheless, the above genus and species analyses yielded a very similar result, which suggests that annual patterns detected at genus level were consistent but somewhat weaker at species level.

When the differences in annual abundance was analysed for each species, a significant increase or decrease was only found in eleven species. These species included *A. pura*, *B. fervidus*, *B. griseocollis, B. impatiens*, *H. confusus, H. modestus*, *L.*

coriaceum, *L. zonulum*, *M. rotundata*, *O. inspergens*, and *S. lateralis*. The only abundant species was *H. confusus*, while the remaining species were common or rare and did not occur in at least one year. Halictids predominated among those species presenting an annual decline in abundance, while 75% of the species that increased belonged to the genus *Bombus*. In terms of absolute abundance, *H. confusus* (ranging from 169 bees in 2003 to just 44 bees in 2008) experienced the most important decline over the years. However, the fact that ten species of this subset did not occur consistently over the four years studied suggests that rarer species are not any less variable than abundant species and may be also more exposed to periodic local extinctions (Pimm *et al.*, 1988). Indeed, several authors have argued that abundant species fluctuate more in terms of abundance than rare species (Glazier, 1986; Gaston, 1998; Owen and Gilbert, 1989). Wolda (1983) suggested that abundant species are not necessarily more variable, but their impact on the bee community is more noticeable. Thus as Wolda (1983) indicated, rare species have an apparent low variance as a result of a statistical artefact caused by their low sample size and their numerous zero values.

The hypothesis that the proportion of bees according to site and disturbance level would vary among years was supported. In 2003, the difference between the number of bees collected at the low disturbance sites (BrockNW and BrockS) and at the high disturbance sites (Pond and St. Davids) was the greatest; this difference declined over the years to its minimum in 2008. Movements of bees would have contributed to decreasing the existing differences, as disturbance levels homogenized, among the four sites (Hanski, 1982a). Hence, bees would have survived at the shelters provided by Brock NW and BrockS in 2003, moving to Pond and St. Davids when habitats of the latter became

similar to those of the former over the years. This is in agreement with the study of Potts *et al.* (2003b), who analysed the effect of disturbance in bee communities over time, and reported a rapid recovery in diversity of both flowers and bees two years after a fire.

4.5. The diversity of the bee community

Halictidae and Megachilidae bees predominated over other families, and their influence was also reflected in the remaining categories (nesting guild, social habit and voltinism). This was mostly due to the contribution of two species, *A. aurata* (Halictidae) and *O. conjuncta* (Megachilidae) that represented over 48% of the 8139 bees analysed for the four years studied. Nonetheless, other taxa also contributed to the overall diversity pattern such as the genera *Andrena*, *Hylaeus* and *L. (Dialictus)*, in addition to *Ceratina calcarata*, *C. dupla/mikmaqi*, *Halictus confusus*, and *H. ligatus*.

4.6. Annual variation in diversity

The generic and species richness that was observed represented only a portion of the total diversity present each year, as not all the genera and species that were present at the sites could be collected. Nonetheless, the results supported the hypothesis that the total generic and species richness present would change annually, with similar annual variation for the total number of genera and species. For the overall four years studied, the observed number of genera (26) and species (57) were close to the estimated total richness of genera (27) and species (62). In 2003 and 2004, a greater number of genera and species could have been collected, as suggested by the difference between the observed and estimated values and the high upper confidence interval values. Conversely,

the 2006 and 2008 estimates were closer to the observed values, suggesting that almost all the genera and species that were present were collected.

Moreover, the results of this study also supported the hypothesis that the generic and species richness that was actually recorded would also vary among years. This was first tested using rarefaction analyses that compared the detected generic and species richness according to the number of individuals collected in the smallest samples (those of the year 2008). The rarefaction curves for genera reflected annual differences that resembled those found in species. The only difference was that 2003 was the richest year in terms of genera, while the highest species richness was recorded in 2006. Furthermore, these curves also provided information about whether the sample size had been sufficient to collect all the genera and species present over the four years studied. Accordingly, in 2004 the sample size had been insufficient to collect the total genera and species present.

Subsequently, when the abundance effect was controlled, annual differences in generic and species richness were still detected, with species richness being more variable. The randomisation analysis detected that the number of genera collected was significantly lower than expected in 2008, while the number of species collected was significantly lower than expected in 2003, 2004 and 2008. Richardson and Richards (2008) reported that in samples in which many rare species are present, observed species richness is significantly higher than expected. This is in agreement with the results of this study, in which the observed richness was significantly lower than expected when the number of rare genera or species was also low. Thus in 2008, only two rare genera were collected, while in 2003, 2004 and 2006 the number of rare genera was between 5 and 6. Conversely, the number of rare species in 2003 (14 species), 2004 (16 species) and 2008

(7 species) was lower than in 2006 (21 species), which was a very speciose year. Furthermore, the randomisation analysis proved to be a good tool to identify in which years the annual differences in generic and species richness occurred.

In terms of community turnover, several studies have reported that genus and species turnover increases with years; these studies were made on bees and other insect communities and had sampling periods ranging from 3 years to over a century (Hanski, 1990; Petanidou *et al.*, 2008; Williams *et al.,* 2001). In this study, genus and species composition increasingly differed with time, supporting the hypothesis that genus and species turnover would increase with years. The similarity of genus and species composition progressively decreased over time, with the highest similarity for periods of less than 3 years and the minimum for the 5-year period, when fewer genera and species were shared. This pattern of decreasing composition similarity was the result of increasing annual turnover of genera and species to which the bee community was subjected. Nonetheless, this pattern was more consistent for species than for genera and for periods of 4-5 years than for periods of $\leq$3 years. Furthermore, it could be also predicted that the observed pattern would be increasingly more pronounced if the study period was increased further.

Annual variation was also found when the proportions of bees according to family, nesting guild, social habit and voltinism was compared among years. The families Halictidae and Megachilidae, in addition to the miner and mason guilds predominated over the four years studied, while social and bivoltine bees did so during 2003, 2004, and 2006. The variation of the latter is partly explained by the low number of bees collected in 2008, when solitary and univoltine bees also became predominant. Nonetheless, within

the above categories, relative abundance for the abundant taxa fluctuated more than for the less common taxa, although ranks were generally more stable for the abundant than for the rare taxa. In this regard, Halictidae and Megachilidae, the most abundant families, had a great deal of variation in relative abundance in addition to the highest ranks over the four years studied, while Apidae and Colletidae were less common and variable.

Previous studies by Glazier (1986), Gaston (1998), and Owen and Gilbert (1989) reported that abundant taxa are usually widespread and exploit temporary or fluctuating resources, leading to very variable populations. Conversely, less common taxa use more stable resources and have relatively more localized and less variable populations. These annual fluctuations in bee community abundance may induce changes in diversity from year to year, as has been already observed for other communities (den Boer, 1981; Hanski, 1982a, 1990; Taylor and Woiwod, 1980). Furthermore, the annual variation pattern in the proportion of bees according to family, nesting guild, social habit and voltinism was the consequence of the annual variation of the abundant (and particularly the halictid) taxa. From year to year, the abundant taxa were the most variable, and were also responsible for the overall pattern of annual variation displayed by the bee community.

Nonetheless, several studies analysing annual variation in diversity reported that abundant taxa tend to be more persistent over time and their relative abundance within the community is also more stable than in rare taxa (Collins and Glenn, 1991; Durrer and Schmid-Hempel, 1995; Gibson *et al.*, 1999; Guo *et al.*, 2000; Hanski, 1982b,c). This is related to environmental and demographic factors affecting the regional pool of taxa (Gibson *et al.*, 1999; Hanski, 1982b). Over time, abundant taxa may be able to maintain,

colonise or establish new populations due to a greater pool of specimens than rare taxa, which may more frequently face the likelihood of local extinction (Collins and Glenn, 1991; Durrer and Schmid-Hempel, 1995; Gibson *et al.*, 1999; Guo *et al.*, 2000; Hanski, 1982b,c; Pimm *et al.*, 1988). Consequently, Hanski (1982b) formulated the Core and Satellite Species Hypothesis (CSS), establishing that regional distribution of species is directly linked to local abundance. Under this model, two types of species may be distinguished: core and satellite species (Hanski, 1982b). The core species usually are regionally widespread and locally abundant; conversely, satellite species are more restricted regionally and locally rare.

After its proposal, the CSS model has been consistently applied to predict regional distributions of species based on local abundances at different locations (Durrer and Schmid-Hempel, 1995; Hanski, 1982c; Gibson, 1999). More recently, this model has been also extrapolated to explain temporal distributions of species based on annual abundances and persistence over time (Collins and Glenn, 1991; Guo *et al.*, 2000). In this study, the CSS model was used to predict the temporal distribution of taxa based on patterns of annual stability in relative abundance and the number of years these taxa were present. Accordingly, genera and species were regarded as 'core' when they were abundant or common and were collected in each year. Taxa were regarded as 'satellite' when they were common or rare and were missing in at least one of the years.

This study also found an annual pattern of stability in abundance ranks of genera and species that was related to proportional representation and persistence over time. This outcome supported the hypothesis that abundance ranks for the most abundant taxa would be more stable annually than for rarer taxa. The abundant and the most common genera

(refer to section 3.4) were regarded as core given that they were also collected in each year; conversely, the remaining common and rare genera were sporadically collected, and as a result they were regarded as satellite (Table 14). Consequently, ranks for the core genera were more stable over time than for their satellite counterparts (Fig. 22). A similar temporal pattern of stability in ranks based on relative abundance and annual persistence was also found for core and satellite species. Core species were represented by abundant and the most common species that persisted in each year (Table 15). On the other hand, the remaining common and rare species were missing in at least one of the years, and were considered as satellite. Core species usually had more stable ranks than their satellite counterparts (Fig. 23). However, some satellite species that were rare or not collected in several years, shared the last ranks annually (displaying annual stability). This would represent a statistical artefact, due to the low sample size of satellite species, rather than stability in abundance ranks (Wolda, 1983).

Communities may change over time through arrival and disappearance of satellite taxa, and variability in the abundance of core taxa, regardless of their persistence (Gibson *et al.*, 1999). In general, taxa that were present in each year were also very abundant, while those with less than 10 specimens overall tended to be only present during one or maximum two years. A remarkable exception was the core species *M. latimanus*, which was present during four years with a total of 10 specimens. Alternatively, three relatively common species *L. zonulum*, *M. rotundata* and *A. manicatum* were considered as satellite, since they occurred sporadically. New species such as *O. albiventris* may have recently incorporated to the bee community. This species was tentatively considered as core given that its abundance increased, displaying very stable ranks, since it was first

Table 14. The classification of core and satellite genera was made according to the abundance category and the number of years each genus was collected.

Genus	Abundance category	Years present	Type
Agapostemon	Common	4	Core
Andrena	Common	4	Core
Anthidiellum	Common	1	Satellite
Anthidium	Common	3	Satellite
Anthophora	Rare	2	Satellite
Apis	Common	4	Core
Augochlora	Common	2	Satellite
Augochlorella	Abundant	4	Core
Bombus	Common	4	Core
Calliopsis	Common	3	Satellite
Ceratina	Abundant	4	Core
Coelioxys	Common	2	Satellite
Halictus	Abundant	4	Core
Hoplitis	Common	4	Core
Hylaeus	Abundant	4	Core
L. (Dialictus)	Abundant	4	Core
L. (Evylaeus)	Common	3	Satellite
Lasioglossum	Common	4	Core
Megachile	Common	4	Core
Melissodes	Rare	2	Satellite
Nomada	Common	3	Satellite
Osmia	Abundant	4	Core
Protandrena	Rare	1	Satellite
Stelis	Common	3	Satellite
Triepeolus	Rare	2	Satellite
Xylocopa	Rare	1	Satellite

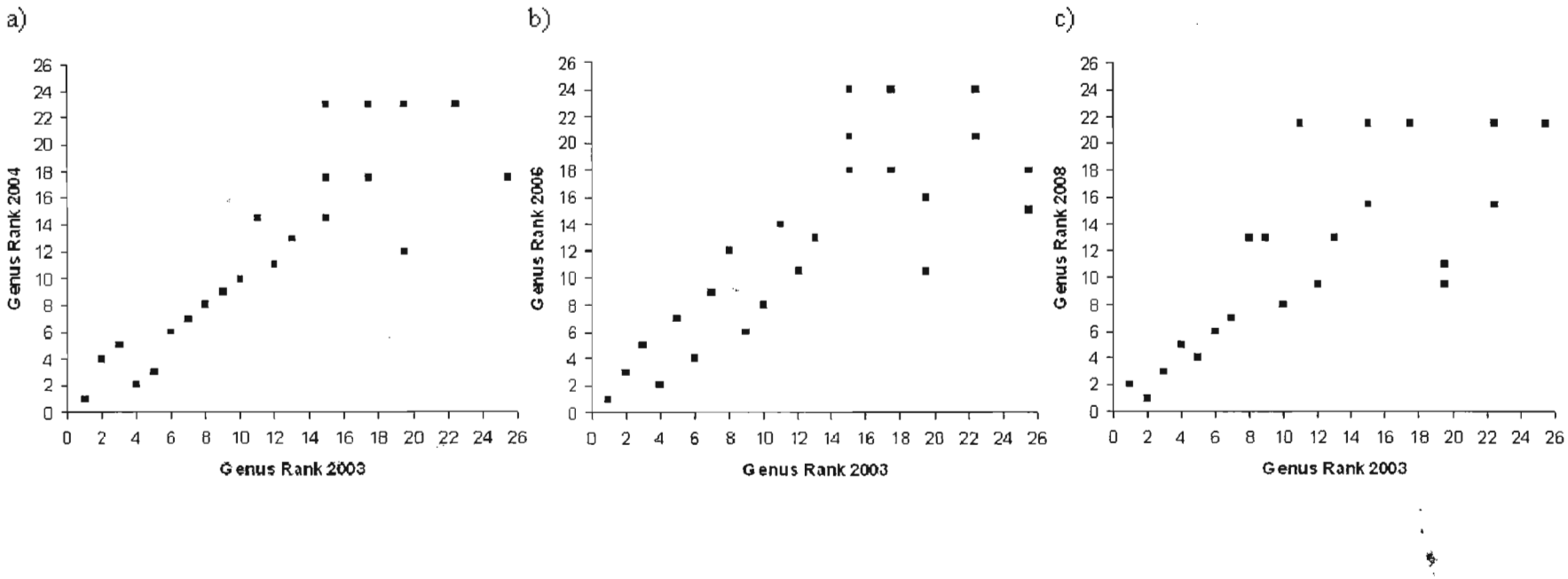


Fig. 22. Annual variation of the rank abundance distribution of genera, in which the distribution of the year 2003 was compared to 2004 (a), 2006 (b) and 2008 (c). Over the years, the ranks of the abundant genera were more stable than those of the less common genera. For each year, ranks were assigned serially starting from the most abundant genus and finishing with the rarest genus. In case of a tie, genus ranks were averaged and the mean was assigned to all the tying ranks.

Table 15. Species were classified as core or satellite based on their abundance category and the number of years they were collected.

Species	Abundance category	Years present	Type
A. manicatum	Common	3	Satellite
A. mellifera	Common	4	Core
A. notatum	Common	1	Satellite
A. pura	Common	2	Satellite
A. striata	Abundant	4	Core
A. terminalis	Rare	2	Satellite
A. virescens	Common	4	Core
B. citrinus	Rare	2	Satellite
B. fervidus	Common	3	Satellite
B. griseocollis	Common	3	Satellite
B. impatiens	Common	3	Satellite
B. mixtus	Rare	1	Satellite
B. rufocinctus	Rare	2	Satellite
B. sandersoni	Rare	1	Satellite
B. vagans	Rare	2	Satellite
C. andreniformis	Common	3	Satellite
C. calcarata	Abundant	4	Core
C. dupla	Abundant	4	Core
C. strenua	Rare	1	Satellite
C. rufitarsis	Common	2	Satellite
H. affinis	Abundant	4	Core
H. annulatus	Common	2	Satellite
H. confusus	Abundant	4	Core
H. ligatus	Abundant	4	Core
H. mesillae	Common	3	Satellite
H. modestus	Common	3	Satellite
H. pilosifrons	Common	4	Core
H. producta	Common	4	Core

Table 15 (Continued)

Species	Abundance category	Years present	Type
H. rubicundus	Common	4	Core
H. spoliata	Common	2	Satellite
H. truncata	Rare	1	Satellite
L. (E.) cinctipes	Common	2	Satellite
L. (E.) macoupinense	Rare	1	Satellite
L. coriaceum	Common	3	Satellite
L. leucozonium	Common	4	Core
L. zonulum	Common	3	Satellite
M. brevis	Common	4	Core
M. centuncularis	Rare	2	Satellite
M. desponsa	Rare	2	Satellite
M. inermis	Rare	1	Satellite
M. latimanus	Common	4	Core
M. mendica	Rare	1	Satellite
M. montivaga	Rare	1	Satellite
M. relativa	Rare	1	Satellite
M. rotundata	Common	3	Satellite
M. texana	Common	3	Satellite
O. albiventris	Common	3	Core
O. atriventris	Common	4	Core
O. conjuncta	Abundant	4	Core
O. inspergens	Common	2	Satellite
O. lignaria	Rare	3	Satellite
O. pumila	Common	4	Core
O. simillima	Rare	1	Satellite
P. andrenoides	Rare	1	Satellite
S. lateralis	Common	3	Satellite
T. simplex	Rare	2	Satellite
X. virginica	Rare	1	Satellite

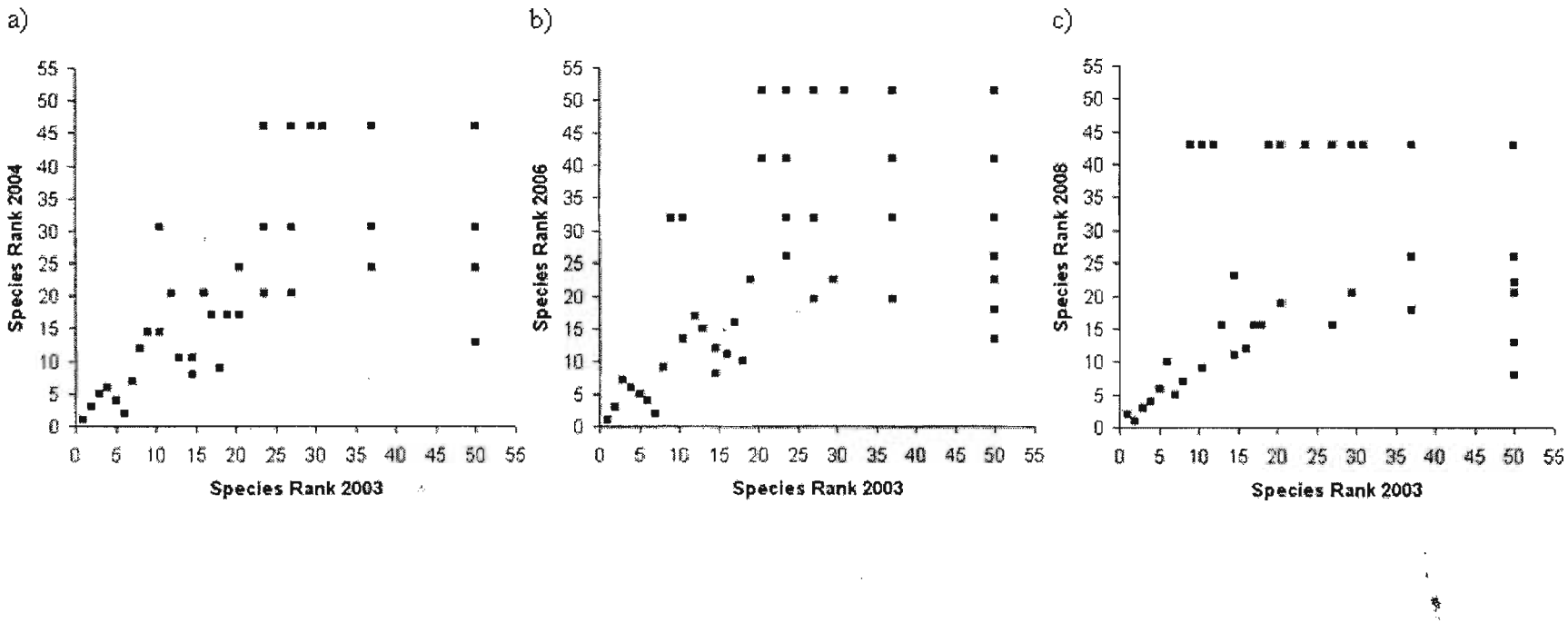


Fig. 23. Annual variation in the rank abundance distribution of species. Rank stability among years was the highest for the most abundant species and decreased as species became less common. Several species not occurring in 2004 (a), 2006 (b) and 2008 (c), and sharing the last ranks, had been either common or rare in 2003. Conversely, several species that were not present in 2003 had occurred in the subsequent years. Each year, ranks were assigned serially starting from the most abundant species and finishing with the rarest species. In case of a tie, species ranks were averaged and the mean was assigned to all the tying ranks.

recorded in 2004. Nonetheless in order to elucidate this aspect, it would have been useful to have data on *O. albiventris* presence in 2005 and 2007. Apidae bees such as the genus *Xylocopa* and some *Bombus* species (i.e. *B. fervidus*, *B. griseocollis* and *B. impatiens*) were un-expectedly rare and sporadic; although this may have been the result of the inability of pan traps to retain large-sized bees upon capture (Cane *et al.*, 2000; Richards *et al.*, 2011).

It should be also noted that, core-satellite roles could theoretically change over time due to stochastic demographic or environmental variation (Hanski, 1982b; Tokeshi, 1992). Therefore, it would be required to monitor over time the abundance and persistence of the core and satellite taxa defined in this study. Nonetheless, I predict that core taxa should be more likely recorded in future samplings than satellite taxa. As the former are expected to be more abundant and persistent over time, while the latter are rarer and sporadically present (Hanski, 1982b).

4.7. Conclusion

This study provided strong evidence of annual variation in phenology, abundance and diversity for this bee community. Inter-annual weather variability may have caused fluctuations in flowering and nesting resources of bees, affecting bee behaviour and phenology over the study years (Gordo and Sanz, 2006; Herrera, 1988; Richards and Packer, 1995; Roubik, 2001; Roulston and Goodell, 2011). In 2003 and 2006, the seasonal flight activity was higher, more advanced, and lasted longer than in 2004 and 2008. Each year, the number of bees collected in spring was higher than in summer, except for 2003. This exception was due to a very high flight activity in 2003 of the

worker brood in bivoltine and eusocial species such as *A. aurata*, *H. confusus*, *H. ligatus* and species of *L. (Dialictus)*, in addition to the adult emergence of *H. affinis* and *H. modestus*.

Over the four years studied, an annual variation pattern in genus and species abundance was detected, with abundant genera and species occurring more consistently than their less common and rare counterparts. In addition, abundant genera and species tended to be in the same abundance group over the years, while less common and rare taxa were more variable. The number of bees collected either per genus or species differed from year to year, displaying a decline over the four years studied, due to the low number of bees collected in 2008. Since the number of bees collected greatly fluctuated among years, this study were extended to cover the longest possible time interval in order to gain full understanding of temporal variation processes (Roubik, 2001). Bee sampling was conducted in only four years of collections; therefore, the detected declining trend might have been an artefact resulting from the relatively short term spanned by this study. Indeed, surveys carried out in 2009 and 2010, using pan traps on a linear transect pattern, would suggest an increase in the number of individuals of this bee community (Richards *et al.*, *unpubl. data*). Furthermore, the existing difference in the number of bees collected at sites of low and high disturbance decreased over the years. A rapid recovery after disturbance and movement of bees among sites may have contributed to lessen and to homogenize differences between sites with different levels of disturbance in the past (Hanski, 1982a; Potts *et al.*, 2003b). Moreover as the time series of this study increases, future disturbances (i.e. mowing) occurring at the four sites would form part of the internal ecological dynamics of their habitat (Rykiel, 1985), this may have already been

the case for the Brock sites. This suggests that the assessment of disturbance effects on bee communities of the Niagara Region, over a longer period of time, would be of great ecological and conservational value.

This study also reported annual variation in diversity, in terms of genus and species richness, composition and persistence of taxa, and in terms of the proportion of bees according to family, nesting guild, social habit and voltinism. Generic and species richness varied annually, following a similar pattern in 2004 and 2008, when the lowest number of genera (16) and species (28) was recorded. In 2003, the highest number of genera was collected (24), while the highest number of species (45) was detected in 2006. Moreover, genus and species turnover increased with years, as bee community composition increasingly differed with time, with lowest similarity values for periods >3 years. This represents an interesting outcome if it is compared with studies that found similar composition in bee communities analysed over a four-decade period (Williams *et al.*, 2001).

Regarding bee proportion, the abundant taxa are more variable than less common taxa (Glazier, 1986; Gaston, 1998; Owen and Gilbert, 1989; Wolda, 1983). In this study, the abundant taxa were largely responsible for the annual variation of the proportion of bees according to family, nesting guild, social habit and voltinism. These patterns were affected by abundance fluctuations of the abundant taxa over the years, which had an important influence on bee community annual variability.

Moreover, the persistence of genera and species over time was related to their relative abundance; therefore, abundance ranks for core genera and species were more stable annually than for their satellite counterparts. Locally abundant genera and species

are also abundant regionally, ensuring a steady supply of individuals to the community, which makes core taxa to occur consistently and to predominate over time (Collins and Glenn, 1991; Durrer and Schmid-Hempel, 1995; Gibson *et al.*, 1999; Guo et al., 2000; Hanski, 1982b,c).

In general, over the four years studied annual variation patterns at the genus level resembled those detected at the species level. This suggests that the exclusion of *Andrena*, *L. (Dialictus)* and *Nomada* may not have greatly results of analyses at the species level. Furthermore, this is in agreement with the study of Rutgers-Kelly (2005), who found that bee species richness, for several studies, was highly correlated to generic richness. Therefore, analyses at the genus level could provide valuable information when identification at the species level is not complete.

Understanding temporal variation processes in bee communities is relevant to assess the extent of the impact caused by diverse anthropogenic disturbances such as those derived from agriculture, industry, urban settlement, species invasions or global warming. This study contributed to improve our knowledge on the temporal variation of a bee community of the Niagara Region. This study may also offer insights for conservation purposes about the effect of anthropogenic disturbances in bee communities. Finally, this study should be extended over a longer period of time and to nearby locations in order to obtain a greater understanding of the temporal variation and the influence of disturbance on Niagara bee communities.

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6. APPENDIX I

6.1. Methods for the analysis of transect pattern effect

6.1.1. Study sites

A test of transect pattern effect was carried out at the 406 site east of the GQNS (latitude: N 43°07.492', longitude: W 79°13.949'). The 406 site is bordered to the north by the Niagara Escarpment, to the east and the south by the 406 highway and to the west by a tree line. The predominant vegetation at the 406 site was formed of set-aside meadows since the 1960s when farming finished and they have been un-mowed for the last two decades. Disturbance levels at the 406 site were regarded as low as assigned in previous surveys (Rutgers-Kelly, 2005; Richards *et al.*, 2011).

The 406 site was selected due to low disturbance and to its rectangular dimensions, where the P140, X050 and X140 patterns could be deployed simultaneously. The closest distance among the three transect patterns was always greater than 20m. This cautious approach, based on observations by Droege *et al.* (2010), was taken in order to avoid pan trap competition among different transect patterns. The addition of the H-like pattern would have provided a greater power to this test; however, site dimensions did not allow for a fourth transect pattern to be deployed. In addition, Droege *et al.* (2010) had already reported that transect pattern shape did not affect the specimen catch rate in their study.

6.1.2. Collection period of specimens

Collections were made on 1 June, 11 June, 21 June and 7 July 2010. The test was initially conceived to be carried out twice, coinciding with the highest peaks of activity of

forager bees of mid-to-late spring and early summer. However, after the low number of bees captured at the first instance (1 June 2010) four collections were carried out.

6.1.3. Bee collections

Collections were performed by R. Kutbi and R. León Cordero using pan traps in the same manner as described in section 2.3. The transect patterns used to test the transect pattern effect on the analysis of bee community structure were P140, X050 and X140.

6.1.4. Bee handling and identification

Upon recovery, pan trap contents were strained, and all the arthropods collected were subsequently poured into three 750 ml plastic containers labelled with the date, the location and the pan trap colour. Once in the laboratory, insects were rinsed with water and temporarily stored in Nasco Whirl-Pak ® bags containing 70% ethanol until sorting. Bee specimens were sorted from other arthropods, pinned and labelled indicating the site, the date, the collection method, the pan trap colour, and the transect pattern. Bee specimens were identified to genus and species following the same procedure as for the years 2004, 2006 and 2008 (please refer to the section "2.4 Bee handling and identification" in the methods).

6.1.5. Field research procedures of the test of transect pattern effect

The first objective of the current study was to test the null hypothesis that the different transect patterns used had no effect on the numbers and types of bees captured. It was important to test whether the P140, X050 and X140 patterns could have differed in

their specimen catch rates (the sampling effort), as this might have influenced the analyses of bee community structure.

6.1.6. Data analysis

Before carrying out the test of the transect pattern effect, it was necessary to determine the minimum sample size required, so that the statistical analysis selected could detect significant differences with an acceptable confidence level. Therefore, an *a priori* test of statistical power was performed for a one-factor ANOVA. The *a priori* test was carried out at different effect sizes (measured in units of standard deviation) as suggested in Cohen (1988): small ($\delta = 0.25$), medium ($\delta = 0.5$), and large ($\delta = 0.75$, 1.0 and 1.25). The statistical power for a hypothetical value of N = 50 bees per transect pattern considering a small, medium and large effect size was 18.1% (for a small effect), 59.3% (for a medium effect) and 92.3%, 99.5% and 99.9% (for the three δ values at which the large effects were considered). The assumptions of normality were tested for date and pan trap colour using the Kolmogorov-Smirnov test. Subsequently, two one-factor ANOVA analyses were performed in order to test significant differences in the number of bees collected per date and per pan trap colour among the three transect patterns. A randomisation analysis was performed in order to test the null hypothesis that the number of bee species collected did not differ among transect patterns. Richardson and Richards (2008) designed the randomisation analysis used in the current study.

6.2. Results

A total of 219 bee specimens belonging to 5 families, 14 genera and sub-genera and 19 species were collected using the P140, X050 and X140 transect patterns (Table 16). The number of bees collected was normally distributed and did not differ significantly among the three transect patterns either per date (Table 17; Kolmogorov-Smirnov analysis: $D = 0.17$, $p = 0.15$; ANOVA: $F_{2,9} = 0.05$, $p = 0.95$) or per pan trap colour (Table 18; Kolmogorov-Smirnov: $D = 0.26$, $p = 0.08$; ANOVA: $F_{2,6} = 0.02$, $p = 0.98$).

The frequency distribution of species generated by the randomisation analysis showed that the observed species richness was not significantly different than expected at P140 (13 species observed; 95% C.I. range: 9.91-16.20), X050 (14 species observed; 95% C.I. range: 9.80-16.08) and X140 (10 species observed; 95% C.I. range: 7.73-14.07) (Table 19). Only 6 species in addition to the sub-genus *Lasioglossum (Dialictus)* were common throughout P140, X050 and X140: *Augochlorella aurata*, *Ceratina calcarata*, *Halictus confusus*, *Halictus ligatus*, *Hylaeus affinis* and *Osmia conjuncta*. Both P140 and X050 shared *Halictus rubicundus*, *Lasioglossum leucozonium* and *Osmia atriventris*. The X050 and X140 patterns had *Apis mellifera*, *Bombus mixtus*, *Osmia pumila*, and the genus *Andrena* in common. P140 and X140 did not share any species in common. Two species were exclusive to P140: *Agapostemon virescens* and *Hoplitis pilosifrons*. Two species were also exclusive to X050: *Ceratina dupla/mikmaqi* and *Lasioglossum coriaceum*. Only *Megachile relativa* was exclusive to X140.

Table 16. Number of bees per taxon (genera and species) collected in each transect pattern (n = 21, for each transect). The identification of those taxa denoted as *sp.* belonging to the genera *Andrena* and *L. (Dialictus)* was completed only to genus and sub-genus level, respectively.

Taxon Name	P150	X050	X150	Grand Total
Agapostemon virescens	1	0	0	1
Andrena sp.	0	1	1	2
Apis mellifera	0	3	1	4
Augochlorella aurata	15	10	7	32
Bombus mixtus	0	1	1	2
Ceratina calcarata	15	8	6	29
Ceratina dupla/mikmaqi	0	2	0	2
Halictus confusus	6	3	3	12
Halictus ligatus	1	1	2	4
Halictus rubicundus	2	1	0	3
Hoplitis pilosifrons	1	0	0	1
Hylaeus affinis	3	9	5	17
L. (Dialictus) sp.	25	24	33	82
Lasioglossum coriaceum	0	1	0	1
Lasioglossum leucozonium	2	2	0	4
Lasioglossum zonulum	1	0	0	1
Megachile relativa	0	0	1	1
Osmia atriventris	1	1	0	2
Osmia conjuncta	2	7	7	16
Osmia pumila	0	1	1	2
Stelis lateralis	1	0	0	1
Grand Total	76	75	68	219

Table 17. Number of bees collected on 1 June, 11 June, 21 June and 7 July of 2010 in each transect pattern deployed at the 406 site.

	P140	X050	X140	Grand Total
01/06/2010	12	16	11	39
11/06/2010	22	29	15	66
21/06/2010	31	27	30	88
07/07/2010	11	3	12	26
Grand Total	76	75	68	219

Table 18. Number of bees collected using yellow, white and blue pan traps in each transect pattern deployed at the 406 site.

	P140	X050	X140	Grand Total
Blue	1	7	4	12
White	37	31	28	96
Yellow	38	37	36	111
Grand Total	76	75	68	219

Table 19. The mean expected species richness was estimated through a randomisation analysis. In addition, the standard deviation and the 95% Confidence Interval (C.I.) of the generated frequency distribution were also calculated. Observed species richness values within the 95% C.I. range are not significantly different to the mean expected species richness. Therefore, the observed species richness for the three transects was not significantly different to the expected estimations.

	P140	X050	X140
Observed Species Richness	13	14	10
Mean Expected Species Richness	13.05	12.94	10.90
Standard Deviation	1.60	1.60	1.62
95% Confidence Interval range	9.91-16.20	9.80-16.08	7.73-14.07

7. APPENDIX II

Table 20. Species composition of a bee community sampled at four sites (BrN/W, BrS, Pond, StD) of the Niagara Region, through the use of pan traps, during the complete season (all-weeks) of the years 2003, 2004, 2006 and 2008. When complete identification to species level in all the years was not possible then species were denoted as sp. This has been the case when the bee either belonged to genera such as *Andrena*, *Dialictus, Megachile*, *Nomada* and *Osmia* or the bee was damaged (*Hylaeus* and *Lasioglossum* sp.). In bold, those species that appear in the list only when all-weeks are considered.

Family	Genus	Species	Nesting guild	Social habit	Voltinism	2003	2004	2006	2008	Grand Total
Andrenidae	*Andrena*	sp.	Miner	Solitary	Univoltine	128	21	26	74	249
	Calliopsis	*andreniformis*	Miner	Solitary	Univoltine	8	1	3		12
	Protandrena	*andrenoides*	Miner	Solitary	Univoltine	1		1	2	4
Andrenidae Total						137	22	30	76	265
Apidae	*Anthophora*	*terminalis*	Carpenter	Solitary	Univoltine	1		2		3
	Apis	*mellifera*	Large cavities	Social	Multivoltine	17	10	21	19	67
	Bombus	***bimaculatus***	Large cavities	Social	Bivoltine	1				1
		citrinus	Kleptoparasitic	Kleptoparasitic		1	1	1		3
		fervidus	Larg cav./grass	Social	Bivoltine	1	2	4	3	10
		griseocollis	Large cavities	Social	Bivoltine		1	4	8	13
		impatiens	Large cavities	Social	Bivoltine	1		1	11	13
		mixtus	Large cavities	Social	Bivoltine			2	1	3
		perplexus	Large cavities	Social	Bivoltine				1	1
		rufocinctus	Large cavities	Social	Bivoltine	1		2		3
		sandersoni	Large cavities	Social	Bivoltine			3		3
		vagans	Large cavities	Social	Bivoltine		2	1		3

Table 18 (Continued)

Family	Genus	Species	Nesting guild	Social habit	Voltinism	2003	2004	2006	2008	Grand Total
Apidae	*Ceratina*	*calcarata*	Carpenter	Solitary	Univoltine	216	53	154	146	569
		dupla/mikmaqi	Carpenter	Solitary	Univoltine	305	70	98	254	727
		strenua	Carpenter	Solitary	Univoltine	2				2
	Melissodes	***apicata***	Miner	Solitary	Univoltine				1	1
		desponsa	Miner	Solitary	Univoltine	1		1	3	5
	Nomada	sp.	Kleptoparasitic	Kleptoparasitic		10		4	10	24
	Triepeolus	*simplex*	Kleptoparasitic	Kleptoparasitic			1	2		3
	Xylocopa	*virginica*	Carpenter	Social	Univoltine	1				1
Apidae Total						558	140	300	457	1455
Colletidae	*Hylaeus*	*affinis*	Small cavities	Solitary	Bivoltine	121	30	796	98	1045
		affinis/modestus	Small cavities	Solitary	Bivoltine	28		9	18	55
		annulatus	Small cavities	Solitary	Bivoltine	3		8		11
		illinoisensis	Small cavities	Solitary	Bivoltine			1		1
		mesillae	Small cavities	Solitary	Bivoltine	7	2		5	14
		modestus	Small cavities	Solitary	Bivoltine	8	4	14	2	28
		sp.	Small cavities	Solitary	Bivoltine				4	4
Colletidae Total						167	36	828	127	1158
Halictidae	*Agapostemon*	*virescens*	Miner	Social	Univoltine	14	4	17	9	44
	Augochlora	*pura*	Carpenter	Solitary	Univoltine	5	1			6
	Augochlorella	*aurata*	Miner	Social	Bivoltine	1119	715	1260	575	3669

Table 18 (Continued)

Family	Genus	Species	Nesting guild	Social habit	Voltinism	2003	2004	2006	2008	Grand Total
Halictidae	*Halictus*	*confusus*	Miner	Social	Bivoltine	185	105	251	67	608
		ligatus	Miner	Social	Bivoltine	180	171	469	30	850
		rubicundus	Miner	Social	Bivoltine	18	10	44	16	88
	L. (Dialictus)	sp.	Miner			322	272	89	149	832
	L. (Evylaeus)	*cinctipes*	Miner	Social	Bivoltine	5		2		7
		macoupinense	Miner						1	1
	Lasioglossum	*coriaceum*	Miner	Solitary	Univoltine	8	4	3	1	16
		leucozonium	Miner	Solitary	Univoltine	25	8	18	20	71
		zonulum	Miner	Solitary	Univoltine	40	5	5		50
		sp. damaged	Miner	Solitary	Univoltine		1			1
	Sphecodes	***heraclei***	Kleptoparasitic	Kleptoparasitic				1		1
Halictidae Total						1921	1296	2159	868	6244
Megachilidae	*Anthidiellum*	*notatum*	Mason	Solitary	Univoltine	4				4
	Anthidium	*manicatum*	Mason	Solitary	Univoltine	20	3	16	3	42
		oblongatum	Mason	Solitary	Univoltine			3	2	5
	Coelioxys	***banksi***	Kleptoparasitic	Kleptoparasitic				1		1
		rufitarsis	Kleptoparasitic	Kleptoparasitic			1	10		11
	Hoplitis	*pilosifrons*	Mason	Solitary	Univoltine	31	5	28	61	125
		producta	Mason	Solitary	Univoltine	4	3	8	10	25

Table 18 (Continued)

Family	Genus	Species	Nesting guild	Social habit	Voltinism	2003	2004	2006	2008	Grand Total
Megachilidae	*Hoplitis*	*spoliata*	Mason	Solitary	Univoltine	5		5		10
		truncata	Mason	Solitary	Univoltine		1			1
	Megachile	*brevis*	Mason	Solitary	Univoltine	18	13	64	7	102
		campanulae	Mason	Solitary	Univoltine			1		1
		centuncularis	Mason	Solitary	Univoltine			2	1	3
		inermis	Carpenter	Solitary	Univoltine			1		1
		latimanus	Miner	Solitary	Univoltine	1	2	11	1	15
		mendica	Mason	Solitary	Univoltine	1				1
		montivaga		Solitary	Univoltine			3		3
		relativa	Mason	Solitary	Univoltine			6		6
		rotundata	Mason	Solitary	Univoltine	30	1	2	2	35
		texana	Mason	Solitary	Univoltine	3		11	4	18
		sp.		Solitary	Univoltine			1		1
	Osmia	*albiventris*	Mason	Solitary	Univoltine	1	6	15	31	53
		atriventris	Mason	Solitary	Univoltine	24	3	34	18	79
		conjuncta	Mason (shells)	Solitary	Univoltine	582	133	453	504	1672
		inspergens	Mason	Solitary	Univoltine			1	15	16
		lignaria	Mason	Solitary	Univoltine	1		1	1	3
		pumila	Mason	Solitary	Univoltine	71	7	39	37	154

Table 18 (Continued)

Family	Genus	Species	Nesting guild	Social habit	Voltinism	2003	2004	2006	2008	Grand Total
Megachilidae	*Osmia*	*simillima*	Mason	Solitary	Univoltine	1				1
		sp.	Mason	Solitary	Univoltine		1		10	11
	Stelis	*lateralis*	Kleptoparasitic	Kleptoparasitic		5	3	6	1	15
Megachilidae Total						802	182	722	708	2414
Grand Total						3585	1676	4039	2236	11536